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The Size-Biomass Allometry of Forest Trees: A Global Meta-analysis, Novel Methods for Estimating Forest Biomass and a case study of *Fagus moesiaca* Cz.

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DECLARATION

This thesis has been composed by myself from results of my own work, except where stated otherwise, and has not been submitted in any other application for an academic degree.

Dimitris Zianis

April, 2003

Dedicated to the memory of my brother
Γιώργου who died in a working accident.

My business is to teach my aspirations to conform themselves to fact, not to try and make facts harmonise with my aspirations. Science seems to me to teach in the highest and strongest manner the great truth which is embodied in the Christian conception of entire surrender to the will of God. Sit down before fact as a little child, be prepared to give up every preconceived notion, follow humbly wherever and to whatever abysses nature leads, or you shall learn nothing. I have only begun to learn content and peace of mind since I have resolved at all risks to do this.

Huxleys' reply to Kingsley
after the death of his son
23/09/1860

ABSTRACT

An improved knowledge of the processes defining the maximum size of trees is urgently needed to understand the influences of climatic changes on forest resources. Recent theoretical models based on fractal geometry and biomechanical principles predict that unique global relationships exist between several structural and functional characteristics both within and among trees, irrespectively of site conditions and study species. However, theoretical arguments and empirical evidence do not support the outcomes of the aforementioned models.

A global meta-database of allometric equations that relate aboveground biomass to stem diameter was created to test the performance of the aforementioned theoretical models. Statistical analysis indicated that there is a large deviation between theoretical values and empirical data and a biomechanical model was developed in order to capture the variability of the empirically formulated scaling relationships. The biomechanical model supports that trees growing within a forest environment exhibit size-shape relationships so as to avoid exceeding the safety factors against buckling imposed by the mechanical properties of wood tissue.

In addition, a straightforward model was developed, based on fractal analysis, in order to mathematically describe this size-shape correlation for different tree species. Assuming that tree shape 'obeys' different scaling relations in response to the physical forces acting upon it, the dimensional relations of individual trees are accordingly adjusted to follow global rules. The formulated model can contribute in understanding the meaning of the parametric values in the scaling relationships between the various dimensions of trees, as commonly reported in numerous empirical equations. A simplifying method for estimating forest biomass was also derived through this reductionist model. A new technique (called SSS) which predicts dry aboveground biomass values at stand level is also presented in this Thesis. The statistical properties of scaling equations are coupled with the information available in the global database of allometric regressions in order to obtain biomass predictions with minimum effort (harvest of small trees is only required).

Moreover, a field study was conducted in a Mediterranean beech forest (*Fagus moesiaca* Cz.) located in northern Greece, in order to build scaling relationships among several dendrometric characteristics of the study trees. The equations were subsequently used to estimate primary production of the study ecosystem. Carbon isotope analysis of collected leaves and foliar nitrogen concentrations were used to understand the influence of environmental factors on the aboveground primary production in this forest.

Last but not least, a meta-database of stem volume and biomass equations for major European tree species was also built and presented in this Thesis. The meta-database was developed in the context of the European-funded project COST E21, *"The contribution of forests and forestry to mitigate greenhouse effects"*.

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Chapter 6: GENERAL DISCUSSION

LIST OF ABBREVIATIONS

ANPP	Aboveground NPP
ANOVA	Analysis of variance
CF	Correction factor
CI	Confidence interval for statistical parameters
MAI (m^3 ha^{-1} a^{-1})	Mean annual increment of stand volume
MPD	Mean percentage difference (%)
MPDP	MPD for power function (based on two trees)
MPDREG	MPD for the regression equation (based on several trees)
MPDSSS	MPD for the SSS method
NPP	Net primary productivity
OLS	Ordinary least squares
PD	Percentage difference between modelled and observed values
PDB	Belemnite in Pee Dee formation
RMA	Reduced major axis
SE	Stem efficiency
SEE	Standard error of estimate
SSE	Sum of square for error
SSS	Small trees sampling scheme
WBE	Model developed by West *et al.*, 1999.

LIST OF SYMBOLS

Greek Alphabet

Δ	Carbon isotope discrimination
ΔB_S (Mg ha^{-1} a^{-1})	Standing biomass increment
ΔB_h (Mg ha^{-1} a^{-1})	Standing increment of harvested trees
δ	Fractionation ratio
δ_a	The δ value for source atmospheric CO_2
δ_p	The δ value for plant tissue
Π (%)	MPD
ρ (kg m^{-3})	Stem wood density
σ (cm^2 g^{-1})	Specific leaf area

Roman Alphabet

a	Scaling coefficient in M-D allometry ($M = aD^b$)
A (m^2)	Area of the stem cross-section at breast height
a^*	Scaling coefficient in M_S-D allometry
a_{cr}	Scaling coefficient in H_{cr}-D allometry
a_{red}	Scaling coefficient in M-D allometry ($M = a_{red}D^{bred}$) estimated from the 'reductionist' model
a_{reg}	Scaling coefficient in M-D allometry ($M = a_{reg}D^{breg}$) estimated from the regression approach based on several trees
b	Scaling exponent in M-D allometry ($M = aD^b$)
B	Bias in allometric regression resulting from log transformation
b^*	Scaling exponent in H-D allometry
B_A (m^2 ha^{-1})	Stand basal area
B_{cr}	Scaling exponent in H_{cr}-D allometry
B_P	Bias in allometric regression as percentage of the unbiased estimate

b_{red}	Scaling exponent in *M-D* allometry ($M = a_{red}D^{bred}$) estimated from the 'reductionist' model
b_{reg}	Scaling cexponent in *M-D* allometry ($M = a_{reg}D^{breg}$) estimated from the regression approach based on several trees
C	Constant of proportionality in H_{cr}-*D* allometry
c_i	CO_2 concentration in the leaf intercellular spaces
c_a	CO_2 concentration in the atmosphere
d	Exponent of D in the equation that relates V_T to D and H ($V_T \propto D^d H^h$)
D (cm)	Tree diameter at breast height
d^*	Scaling exponent in M_S-D allometry
D_B (cm)	Tree diameter at 0.30 m above ground
D_{BR} (cm)	Branch diameter
D_C (cm)	Stem diameter at the base of live crown
E (10^6 kg m^{-2})	Young's elastic modulus of stem
E_C	Elevation class
E_S (kg tree^{-1} a^{-1})	Stem growth efficiency at tree scale
E^S (Mg ha^{-1} a^{-1})	Stem growth efficiency at stand scale
E_T (kg^{-1} a^{-1})	Total tree growth efficiency at tree scale
E^T (Mg ha^{-1} a^{-1})	Total aboveground growth efficiency at stand scale
f	Stem form factor
F	Fractal dimension of an object
G	Percent standard error in allometric regression resulting from the log transformation of the real data
h	Exponent of H in the equation that relates V_T to D and H ($V_T \propto D^d H^h$)
H (m)	Total tree height
H_{cr} (m)	Critical height of tree
H_S (m)	Tree height to the base of the live crown
I	Intercept in the ANOVA
j (m)	Sampling height above ground
K	Parameter in the biomechanical model
L^* (m^2 m^{-2})	Leaf area index

L_A (m^2)	Tree leaf area
L_{BR} (m)	Branch length
M (kg)	Aboveground tree biomass
M_{BC} (kg)	Branch dry biomass in crown
M_{BE} (kg)	Dry biomass of epicormic branches
M_{BT} (kg)	Tree branch dry biomass (including epicormic)
M_{CS} (kg)	The dry mass of the stem within the crown
M_{CW} (kg)	The woody dry mass within the crown ($M_{CW} = M_{BC} + M_{CS}$)
M_{FC} (kg)	Foliage dry biomass in crown
M_{FE} (kg)	Foliage dry biomass of epicormic branches
M_{FT} (kg)	Total foliage dry biomass ($M_{FT} = M_{FE} + M_{FC}$)
M_L (Mg ha^{-1} a^{-1})	Average yearly production of leaf litter biomass
M_S (kg)	Dry biomass of tree stem
M_{Scr} (kg)	Stem mass of a tree with height equal to H_{cr}
M_{SP} (kg)	The dry mass of stem from ground to 0.30 m above ground (stump)
N_A (g cm^{-2})	Nitrogen content values per unit leaf area
N_M (g g^{-1})	Nitrogen content values per unit leaf mass
P (m)	Perimeter of the stem cross-section at breast height
P_R (m^2)	Horizontal crown projection area
P^S (Mg ha^{-1} a^{-1})	Stand aboveground NPP
P_T (kg $tree^{-1}$ a^{-1})	Tree aboveground NPP
Q	Correction factor
R	The absolute isotopic composition of a sample
R_a	The absolute isotopic composition of atmospheric CO_2
R_p	The absolute isotopic composition of CO_2 in plant tissue
R_s	The molar abundance ratio $^{13}C/^{12}C$ of the standard carbon in CO_2 generated from a fossil belemnite from PDB
S	Safety factor
S_B (Mg ha^{-1})	Branch dry biomass at stand scale
S_D (trees ha^{-1})	Stand density
S_F (Mg ha^{-1})	Foliage dry biomass at stand scale

S_P (kg tree^{-1} a^{-1})	Tree stem production
S^S (Mg ha^{-1} a^{-1})	Stem productivity at stand scale
S_S (Mg ha^{-1})	Stem dry biomass at stand scale
S_S (Mg ha^{-1})	Aboveground dry biomass at stand scale
U (m)	Stand elevation
V_S (m^3)	Stem volume
V_T (m^3)	Tree volume (stem + crown)
Z (%)	Stand slope

LIST OF DATASETS

Name	Sample	Place	Use
'Biomass'	Sixteen trees. Complete harvesting of above ground components.	Naousa's forest	Developing empirical regressions (Ch. 4).
'Elevation'	Fifty-four branches (six per tree) collected from nine trees across an elevation gradient.	Naousa's forest	Estimating specific leaf area, nutrient analysis, carbon isotope analysis (Ch. 5).
'Tree ring'	Tree rings from 38 trees (19 dominant and 19 suppressed) were collected.	Naousa's forest	Ontogenetic trends of NPP and L_A at tree scale (Ch. 5).
'Stand data'	Diameter distribution of beech stands collected from Stefanidis in 1991 and 2001.	Naousa's forest	Estimation of stand biomass (Ch. 4) and elevational variability of P^S and L^* (Ch. 5).

1. INTRODUCTION

1.1 TREE ALLOMETRY, STAND BIOMASS AND FOREST PRODUCTIVITY

After a brief absence of about 30 years from scientific research, forest biomass appears to have regained its historical importance, for three main reasons. Firstly, the estimation of standing biomass is required to determine the carbon sequestration by forest ecosystems, and to assess the potentiality of forests as a mitigation option to the increasing atmospheric concentrations of CO_2. A political interest has also arisen, since carbon sequestered in terrestrial ecosystems has become a valued commodity. Thus, there is an increasing need to develop rapid and easily implemented methods in order to estimate the amount of carbon (or biomass, of which *ca* 50% is carbon) that forests contain. Secondly, wood is considered an important renewable energy source as an alternative to fossil fuels. According to Hall (1997), a number of developed countries derive a significant amount of their primary energy from biomass, while numerous environmental and societal benefits derived from biomass energy, compared with fossil fuels, have also been reported. Thirdly, for scientific purposes, standing biomass is frequently used as one of the basic parameters in several ecological and ecophysiological models.

In spite of the fact that individual trees can become very massive (a single *Sequoia* tree can reach up to 250 Mg of dry mass aboveground), Geider *et al.* (2002) speculated that increased CO_2 concentrations will enhance the carbon cycle through forest ecosystems, rather than maximise carbon storage (*i.e.*, biomass accumulation). Since trees can not exceed the upper limit of organic material they are designed to bear, Geider *et al.* (2002) concluded that an

'... improved knowledge of the processes defining the maximum size of trees...'

is required to understand better the effect of elevated [CO_2] and other aspects of climate change on tree growth and forest productivity.

Galileo Galilei is considered to be the first scientist who tried to understand the correlation between biological variables and size, based on first principles. This way of analytically derived relationships leads to a hypothesis very different from that obtained by statistical inference of empirical data. Under this line of reasoning, Metzer (1893, cited in Niklas, 1992) argued that physical forces – such as dynamic wind loading - mainly influence the shape of tree branches. Subsequently, several researchers used first principles derived from engineering theory, in order to understand the interrelationships of tree linear dimensions (McMahon, 1973; King and Loucks, 1978; Niklas, 1992).

However, despite the knowledge on tree size-shape relations, gained from this theoretical work, no real achievement has been made so far to readily estimate tree and stand biomass. Researchers, more often than not, still depend on destructive methods to predict standing biomass and productivity of forest resources (*e.g.*, Bartelink, 1997; Araujo *et al.*, 1999; Bolstad *et al.*, 2001) while information obtained by remotely sensed data (aerial photos and satellite images) has to be validated against empirically derived models (see for example Drake *et al.*, 2002). Recently, West *et al.* (1999) have developed a theoretical model, which relates anatomical and morphological characteristics to physiological processes in individual plants through allometric relationships, in order to understand the mechanisms which drive wood accumulation and primary productivity. However, criticism on their work based on theoretical arguments (Magnani *et al.*, *submitted*; see also Chapter 2) and empirical data (Chambers *et al.*, 2000; Mencuccini, 2002; see also Chapters 3 and 4) restrain the applicability of the model in accurately predicting biomass and productivity of forest ecosystems. Clark *et al.* (2001) pointed out that more datasets on forest productivity are needed in order to understand thoroughly the factors affecting this process.

1.2 AIMS OF THE STUDY

This Thesis examines whether theoretical advances of tree allometry, mainly based on fractal geometry and biomechanical theory, may be readily used to obtain stand biomass predictions and in turn simplify estimations about forest primary production. An empirical study of productivity in a Mediterranean beech ecosystem was also made to illustrate the factors limiting forest production. Specifically, the following objectives have been set and analysed in one or more Chapters of the Thesis.

1. To understand whether randomness or determinism may explain the variability in published allometric equations which relate aboveground tree biomass to diameter at breast height for a number of tree species across the globe.
2. To assess the performance of current theoretical models in estimating standing biomass. Simplifying procedures for predicting dry aboveground biomass at stand and forest scale were also developed.
3. To formulate allometric equations that relate dendrometric characteristics to tree dimensions for *Fagus moesiaca* Cz species growing at Vermio Mountain, Northern Greece.
4. To report the variability of primary productivity values across a *Fagus moesiaca* Cz forest at Vermio Mountain, Northern Greece and to determine the abiotic factors which may limit tree growth.
5. To present a database of stem volume and biomass equations for the major European tree species.

1.3 TREE ALLOMETRY

The relationships among different processes or components of a physical or biological system should be adjusted in relation to size changes in order to prevent malfunction. The range of size-correlated botanical phenomena is vast, but it should

be noted that size is not the driving force of changes in form and processes (Niklas, 1994). D'Arcy Thompson (1917) clearly pointed out in his book, *On Growth and Form*, that growth in size depends on two types of information, namely the physical-chemical laws and the genetic capacity of the organism. The interaction between environmental and biological variables gives organisms the ability to maintain the same relationships among critical structural and functional variables over a wide range of scales (Brown *et al.*, 2000). According to Niklas (1994), scale refers to the proportion that a representation of an object or system bears to the prototype of the object or system, and under the neologism introduced by Mandelbrot (1983), such self-similarity is said to be a fractal.

1.3.1 Statistical properties of allometric equations

In mathematical terms, scaling relationships take the form of the power function which has been so well established in the study of biological phenomena, that it is called an allometric equation (Huxley, 1932). If the dependent variable Y is non-linearly related to the independent variable X, then the following formula expresses the interdependency between them:

$$Y = aX^b \qquad \text{Eq. (1.1)}$$

where a is a normalisation constant and b is the scaling slope, which takes a value different from one. In the case that $b = 1$ then an isometric relationship exists between Y and X. When both variables are plotted on logarithmic axes, a linear relationship is obtained:

$$\ln Y = \ln a + b \ln X \qquad \text{Eq. (1.2)}$$

where b is the slope and $\ln a$ the intercept of the line. The linear property of the log-transformed allometric variables, permits us to use the ordinary least squares (OLS) regression analysis (also called Model I regression) to parameterise Eq. 1.2. Model I

regression makes three assumptions about empirically obtained datasets (Niklas, 1994):

1. The values of the X variable are free from errors.
2. The values of Y for a specific value of X are independent and normally distributed.
3. Samples of Y along the regression line have a common variance, that is the variance of the random deviation of the error term. This term is assumed to be normally distributed with a zero mean value and its variance independent of the magnitude of Y or X.

Applying OLS to the log-transformed data, an empirical value of $\ln a$ is obtained; however a bias is introduced when we use the antilog to estimate the Y values on the linear scale (Finney, 1941; Beauchamp and Olson, 1973; Sprugel, 1983). This bias derives from the fact that the mean in the log-transformed Y values is the median of the distribution in the untransformed Y values, and this is obviously not arithmetically equal to the mean. In tree biomass studies this bias introduces an error of less than 10% and a formula for the correction factor which eliminates this deviation was reported by Sprugel (1983).

Although the OLS regression has a predictive power (*i.e.*, estimates the mean value of Y for a specified value of X), it underestimates the value of the scaling exponent, b (Niklas, 1994). Since there is natural variation and measurement error in the X variable, Model II regression analysis (or reduced major axis, RMA) was developed to overcome the bias introduced by these pitfalls. Model II regression analysis typically establishes a more reliable estimate of the scaling exponent which is useful in studies where comparisons among different datasets are made. I will not further elaborate on the assumptions and techniques applied in Model II regression since standard statistical textbooks offer a detailed account of the subject. Model I regression was used to develop empirical equations for the studied beech trees (Chapter 4) and to relate aboveground primary productivity to leaf area index and

elevation (Chapter 5). The RMA approach was applied in Chapter 2 to compare empirical allometric constants to theoretical values.

1.3.2 Theoretical approaches to allometric equations

Allometric relationships have played a central role in zoological research, but only a few botanical studies have tried to explain the scaling interrelations among different tree characteristics (Niklas, 1992; Niklas, 1994; West *et al.*, 1999). Niklas' approach gives emphasis on the principles of physics and engineering to answer fundamental questions about the relation between plant form and function, implying that limits set by the environment drive the growth, reproduction and evolution of green organisms. This kind of analysis initiated with the assumption that trees and plants are mechanically designed in such a way so as to sustain forces imposed by external factors and self-loading pressures (*Biomechanical theory*).

On the other hand, West *et al.* (1999) attacked the 'allometric' problem - *i.e.*, why do we obtain scaling relations in quantitative plant studies - within a geometrical framework. They tried to integrate biomechanical constraints posed by static forces, with an optimum distribution system of biological resources (see also West *et al.*, 1997). They used three parameters to quantify the distribution network through the relationship of daughter to parent branches:

1. The ratio of daughter to parent branch radii, which equals $n^{-\alpha/2}$
2. The ratio of daughter to parent vessel tube radii, which equals $n^{-\beta/2}$
3. The ratio of daughter to parent branch length, which equals $n^{-1/3}$

where n is the number of daughter branches derived from one parent branch (which is assumed to be two) while the parameters α and β are related to mechanical constraints and to the minimisation of hydraulic resistance, respectively. This model (hereafter WBE model) predicts several allometric relationships between structural and functional characteristics, both within and among individual plants. The WBE model has also been used to understand the interplay of anatomical and physiological

effects of an individual tree at the marco-ecological and evolutionary scales (Enquist *et al.*, 1999; Enquist *et al.*, 2000; Enquist and Niklas, 2001; Niklas and Enquist, 2001).

1.3.3. Fractal geometry and tree allometry

Nowadays, scaling relationships between variables describing natural phenomena are analysed through the medium of fractal geometry introduced by Mandelbrot (1983). Traditionally, length, area, and volume in forestry studies have been estimated with tools provided by Euclidean geometry. However, natural occurring objects such as branches, basal areas, and tree crowns, are better described by a generalisation of classical geometry, called fractal geometry (Zeide, 1991). Fractal geometry was developed by Mandelbrot (1983) and is increasingly applied to almost all branches of science. Quoting Zeide (1991)

'...some foresters might respond to the term 'fractal' with: "what broke?" If this question is to be taken seriously, the answer would be: the hold of ancient geometrical concepts on our understanding the nature'.

Zeide (1991) also believes that fractal geometry can play a significant role in describing forms of stems, crowns and root systems. The fractal dimension of each tree can be estimated and related to variables that can facilitate our understanding of tree growth and structure. In addition, Mandelbrot (1983) in his book uses many examples of tree structures in order to explain fractal dimensions of branching patterns. Fractal geometry has enforced a new perspective to dimensionality of natural objects. Euclidean dimensions do not provide insight when a tree crown and a room are compared. Both of them have a dimension of three and no information can be obtained about the structure of the objects under investigation. On the contrary, fractal dimensions and related parameters could play a significant role in ecological research (Zeide and Gresham 1991; Zeide and Pfeifer,1991; Berezovskava *et al.*, 1997; Horn 2000), mainly based on their ability to express the inner fabric of natural objects and phenomena (Zeide, 1993).

1.3.3.1 Fractal dimensions

Idealised objects (straight lines, rectangles, cylinders) belong to spatial dimensions that are described by integer numbers (lines = 1, surfaces = 2 and solids = 3). As a result, length, area and volume in classical geometry are independent of the measurement unit. There is no difference in measuring a straight line with either yards, feet or meters. However, measuring a coastline with progressively smaller units will result in larger estimates of length. Mandelbrot (1983) reports a confusing situation for the common border between Spain and Portugal. A Spanish encyclopaedia estimated this border as 987 km while Portuguese arrived at a longer length for the same border, 1214 km, obviously using smaller units. The spatial dimension represented by the exponent of the relationship between the number of units and the linear unit size can be used to overcome the aforementioned abnormality. Imagine a straight line with length L, equal to unity, divided into N smaller segments, each n in length. Thus, $L = Nn = 1$ resulting in $n = 1/N$.

Following the same reasoning, $A = Nn^2 = 1$, and $n = 1/N^{1/2}$, where A is the area of a surface equal to unity with side length L, and finally $V = Nn^3 = 1$, with $n = 1/N^{1/3}$, where V is the volume of a solid equal to unity with side length L. Examining these equations we can see that the exponent of n in each case is a measure of the similarity dimension, F, of the object (Addison, 1997), and in general

$$Nn^F = 1 \text{ or}$$
$$F = \ln(N)/\ln(1/n) \qquad \text{Eq. (1.3).}$$

Since fractal geometry is a generalisation of classical geometry, the last expression may also be used to produce dimensions of fractal objects where F equals a non-integer number (Mandelbrot 1983). Thus, many irregular, rugged, and ramified shapes 'belong' to dimensions that can be considered as a number between one and three. Particularly the dimensions of natural lines (*e.g.* branches, boundaries of forest types, *etc.*) are bounded by one and two, implying that they can be described as

hybrids of ideal lines and surfaces (Zeide, 1991). In the same way, a tree can be described as a surface with a dimension limited by two and three, because of the fractal properties of crown and roots. According to Addison (1997) fractals themselves have their own dimension, known as fractal dimension, which is usually a non-integer dimension.

1.3.3.2 Fractal dimension and tree crowns

More detailed crown architectural information has only recently been used to model tree crowns with individual branches, leaves or shoots using the technique of fractal geometry (Berezovskava *et al.*, 1997; Horn 2000). Addison (1997), defines the mathematical fractals as the structures that comprise exact copies of themselves at all magnifications. Of course we do not expect to meet such structures in nature since each small fraction of an object is not identical to the whole. However, these natural objects or random fractals contain a statistical element of self-similarity. This means that each small part of a random fractal has the same statistical properties as the whole but only for a certain range of scaling (magnification).

Tree crowns exhibit similarity of a part to the whole. Each branch resembles branches in the higher and lower orders, assuming an iteration of underlying biological processes resulting in structure within structure. The quantification of fractal dimension relies on the determination of segments with variable lengths that are needed to cover the object under investigation. This method is called the box-counting method and is widely used in natural sciences. For tree crowns, this approach would require subdividing the crown into cubic boxes, counting the boxes containing at least a leaf, and repeating this procedure for several sizes of boxes. The number of counted boxes is regressed on their sizes and finally the fractal dimension is obtained.

This method is not feasible for estimating the fractal dimension of a tree crown. In order to overcome this problem, Zeide and Pfeifer (1991) developed 'the two-surface' method for the estimation of tree crown fractal dimension. It is based on the

assumption that foliage mass and crown surface area are related through a parameter called the fractal dimension of the tree crown. Thus, $L_A = wE^{F/2}$ where L_A is the leaf area of the tree, E is the surface area of a convex hull that envelopes its crown, and w is a constant. If the volume, V, of the convex hull, that envelops the crown is available, then $L_A = qV^{F/3}$, where q is a constant. Both $E^{F/2}$ and $V^{F/3}$ should be considered as the average linear size of the crown (*i.e.*, the average of all crown widths and lengths). In order to extend the usefulness of their method they had to prove that

i) tree crowns of the same species and class are geometrically similar and
ii) tree crowns are self similar objects.

Using data from dominant trees of 10 conifer species measured in the Rocky Mountains by Brown (1948; cited by Zeide, 1993), foliage mass (which is proportional to leaf area) was regressed on the crown volume on log-log scales. The relationship obtained was linear and never contained points of inflection. This outcome is consistent with self-similarity of tree crowns. In other words, it is implied that in statistical terms tree crowns of the studied species do not change shape. It may even be suggested that for coniferous species, crown shape is invariant in a phylogenetic context. In addition, Zeide and Pfeifer (1991) concluded that tree crowns of the same species and class can be considered similar in a geometrical sense.

Moreover, in a study of fractal dimensions of three loblolly pine plantations in coastal South Carolina, Zeide and Gresham (1991) suggested that this variable may be sensitive to site quality. In stands with high potential for wood production, tree crowns had the largest fractal dimension. The reported dimensions ranged from 2.74 to 2.45. Idealised extremes of crown fractal dimension reflected by 2.0 and 3.0. A dimension of 2.0 would indicate that foliage mass is exactly proportional to the area of convex hull that envelopes the crown, and thus in turn implies that the foliage is located exclusively on the crown periphery. On the other hand, when the crown

fractal dimension is 3.0, the foliage mass is proportional to the volume of the convex hull and is distributed uniformly throughout the crown volume (Zeide, 1991).

In reality, it is to be expected that crown dimension will vary between 2.0 and 3.0, influenced by several genetic and environmental variables (Zeide and Gresham, 1991). A correlation between fractal dimension and crown class is also to be expected, provided that trees belong to the same species. Foliage of a suppressed tree tends to be concentrated on the crown's periphery since it is shaded by dominant trees and the tree is not able to maintain foliage in the interior of the crown. Bearing this in mind, a tree crown should be regarded as a hybrid of surface and volume, with an intermediate dimension (Berezovskava *et al.,* 1997). A new approach for estimating total aboveground biomass of forest stands based on fractal analysis of trees will be presented in Chapter 2.

1.4 FOREST BIOMASS STUDIES

Allometric equations have been extensively used in forest biomass studies, for both scientific reasons (studying the energy and nutrients flows in ecosystems), and for the sustainable planning of forest resources. In this Section, a brief historical background on biomass studies is given and definitions and methods for estimating stand biomass are presented. According to the *Terminology of Forest Science* (1971), biomass is generally defined as

'The total quantity, at a given time, of living organisms of one or more species per unit area (species biomass) or of all species in a community (community biomass)'.

The biomass is commonly measured in terms of dry mass. Estimation of forest biomass has been pursued for both practical forestry issues and for scientific purposes. Planners at strategic and operational levels have strongly emphasised the need for accurate predictions of tree biomass, while Hall (1997), for example, reviewed the potential role of biomass as an energy source in the 21st century.

Historically, the Flemish physician and chemist, van Helmont (1577-1644), is considered to be the first who did a plant physiology experiment which involved biomass measurements (cited by Stern, 2000). He planted a willow branch weighing 2.3 kg in an earthenware tub filled with 74.4 kg of dry soil. Five years later he reweighed the willow, which had gained 60.68 kg, while the soil weight was 56 g less. At the stand scale, Kittredge (1944) reported that leaf biomass plays a major role in affecting light penetration, rainfall interception and transpiration. During the 1950s, biomass studies were carried out in Japan (for a full reference list, see Satoo and Madgwick, 1982), and in Britain (Ovington, 1957; Ovington and Madgwick, 1959) while in the late 1960s the International Biological Programme, run by UNESCO, expanded the biomass studies throughout the world. The oil crisis in 1973 led to the consideration of renewable natural resources as an alternative option and woody biomass was considered to be one of the most appropriate solutions to the problem. Since then forest biomass studies have been made in almost all biomes covering both tree and shrub species.

1.4.1 Methods for stand biomass estimation

The estimation of forest biomass is a time consuming and very laborious operation. There are three accepted approaches for estimating this variable:

i) The regression analysis, which is the most widely used method and requires destructive harvest of sample trees. The obtained empirical model is subsequently applied to the stand scale and predictions of biomass are therefore obtained. Detailed information on the procedures has reported by Ogawa and Kira (1977), Parde (1980), and Satoo and Madgwick (1982).

ii) The mean tree method, where some 'average' trees are sampled and the mean biomass of these trees is determined. Thus, the stand biomass is calculated as the product between the number of the trees and the obtained mean value (Ovington, 1956).

iii) The unit area method where the total biomass of sample plots is determined and the average biomass per unit of ground area is determined. Finally, this

value is multiplied by the total forested area and the stand biomass is obtained (Satoo and Madgwick, 1982; Chave *et al.*, 2001).

Remotely sensed data have also been used to estimate forest biomass indirectly (Drake *et al.*, 2002; Montes *et al.* 2000). However, these techniques still depend on equations that relate the recorded variable with tree biomass, while calibration of data is usually based on predictions made by allometric equations. Parresol (1999) developed new statistical techniques and procedures to estimate woody biomass at the stand scale and reviewed several statistics for evaluating and comparing biomass models. Cannell (1983) has compiled biomass and production data from forest ecosystems across the globe for different tree compartments, while Parde (1980) thoroughly reviewed several aspects of forest biomass studies. In their textbook, Satoo and Madgwick (1982), presented a quite extensive methodology for biomass estimation while an effort was made to focus on the major ecological variables affecting primary productivity and standing biomass of forest resources.

1.5 A DATABASE OF BIOMASS AND STEM VOLUME EQUATIONS FOR MAJOR EUROPEAN TREE SPECIES

The wealth of allometric equations that relate stem volume as well as biomass of several tree compartments to diameter at breast height, D, has never been summarised for European tree species, contrary to American (Tritton and Hornbeck, 1982; Ter-Mikaelian and Korzukhin, 1997) and Australian trees (Eamus *et al.*, 2000; Keith *et al.*, 2000). Maybe the greater difficulty of such an exercise arises from the fact that the vast majority of the information has been published in the 'grey' literature (forestry and ecology schools, relevant institutes and research centres) across Europe. To overcome this problem, researchers throughout Europe were kindly asked to provide any allometric equations available to them, through the activities of COST E21 Action.

This Action takes part within the European Co-operation in Science and Technology Programme and focus on the quantification of carbon storage in the European forest ecosystems. It also puts emphasis on the understanding of linkages between human activities and climate change, particularly the role of forests and forestry. COST E21 integrates natural, socioeconomic as well as methodological aspects relevant for reporting under the United Nations Framework Convention on Climate Change and the Kyoto Protocol (Laitat *et al.*, 2000). It is scheduled for a four year period (1999-2003).

In October 2001 the Working Group 1 of COST E21, agreed in Liege to develop a European-wide database incorporating functions for stem volume and biomass estimation for different tree components (total above ground, branches, foliage, etc). At the same time theoretical analysis of biomass scaling relationships was being carried out as a part of this Ph.D, and empirical information was needed to validate the developed models. Thus, a joint effort took place between Edinburgh University and the Finnish Forest Research Institute (with A. Lehtonen, R. Makipaa, P. Muukkonen and J. Varyeda). A preliminary version of the database was presented at the Barcelona meeting of COST E21 (July 2002). The database was then distributed across several forest and ecology research institutes and university departments in order to cover the entire European continent for supplementation.

At the time of writing this Thesis about 400 biomass equations and 80 stem volume relationships have been collected. A copy of the database can be found in the floppy disk attached to the back cover of this Thesis. The compiled relationships may provide an important tool both in ecological sciences and for the sustainable management of forest resources in Europe.

1.6 ABOVEGROUND NET PRIMARY PRODUCTION

Understanding the controls on primary productivity of the biosphere is one of the fundamental aims of global change research (Geider *et al.*, 2002). Whittaker and

Likens (1975) are considered to be the first researchers who presented data of primary productivity at a global scale classified into different biomes. Field *et al.* (1998) reported that forests contribute about 62% of all the terrestrial productivity while the global uptake of carbon by forest ecosystems was estimated to be approximately 3465 x 10^7 Mg. However, without reliable field data, the values obtained by biogeochemical models cannot be thoroughly tested. During the International Biological Programme, developed in the late 1960s, the sequential harvest of sample plots was used to estimate net primary production, but Long *et al.* (1989), have criticised the values obtained by this approach. The main reason is that sequential harvesting provides an estimate of aboveground increment to which an estimate of belowground increment, and other components of tree production must be added.

1.6.1 Definitions and concepts related to NPP

The term of net primary production appears to vary among researchers according to their academic background. Thus, a plant physiologist would define that net production is the difference between the total amount of organic matter produced by photosynthesis and respiration losses (Stern, 2000). On the other hand, a forester may define net production as the change in standing crop (usually measured in units of merchantable volume) between two measurements or, in his terms, current increment. Finally, an ecologist would incorporate losses due to herbivory, litterfall, root turnover and death to estimate net primary production of forested ecosystems (Kimmins, 1997).

Primary productivity is the rate at which energy is converted into biomass. Roy and Saugier (2001) defined net primary productivity (NPP) as the actual accumulation of biomass after some of the products of photosynthesis are expended for the plant's own maintenance through respiration. In other words, NPP is the time-integrated value of the net tree photosynthesis. However, in practical terms it is very difficult to measure these variables at an ecosystem scale, and significant uncertainties may easily arise. In order to clarify the underlying concepts of forest productivity, Clark

et al. (2001) have provided a complete and internally consistent framework to guide efforts toward improved estimates of forest NPP.

In a theoretical context, Jarvis and Leverenz (1983) identified six properties of forests which can have substantial effects on growth, while Ågren (1985) presented a theory for plant production derived from the nitrogen productivity concept. Researchers have also tried to understand the productivity of forest ecosystems at various spatial and temporal scales through the development of mechanistic models (see reviews by Ågren *et al.,* 1991; Thornley and Cannell, 1996). Empirical studies have demonstrated that aboveground NPP (ANPP) of forests is related to foliar nitrogen concentration (Birk and Vitousek, 1986; Matson *et al.*, 1994; Schuur and Matson, 2001), leaf area index (defined as the photosynthetic area per unit ground area; Gholz, 1982; Hedman and Binkley, 1988; Fassnacht and Gower, 1997; Bolstad *et al.*, 2001), site quality (Waring *et al.*, 1980), genetic variability (Oleksyn *et al.*, 2000), and stand hydraulic conductance (Mencuccini and Grace, 1996).

1.6.2 Methods for estimating forest ANPP

Net primary productivity is measured per unit of time, which implies that two – or more – successive measurements have to take place. The most common method to estimate aboveground biomass increment (ANPP) is by applying the regression equations (see Section 1.4.1) to the diameter distribution of all trees in the plot. Clark *et al.* (2001) reported two different approaches when allometric relationships are used for estimating stand productivity. In brief, the first approach is based on the recording of growth of individual trees. All the live trees are cored, width of annual rings are measured and biomass increment is obtained through the allometric equations applied to the core readings. Adjustment for ingrowth (young individuals that enter the stand during the period that ANPP is measured) should also take place. In the second approach, total aboveground biomass of a stand is calculated at the beginning and at the end of a specified time interval through repeated measurement of tree diameters. The difference of the two aboveground biomass values is divided by the time period and ANPP is therefore obtained after corrections for ingrowth and

mortality. The second approach is often used when large-scale forest inventory data are available (Schulze *et al.*, 1999).

1.6.3 Aboveground NPP and carbon isotope discrimination

Since the biochemical processes driving the discrimination of assimilated carbon in plants were successfully modelled (Farquhar *et al.*, 1989), ecologists have often used this approach to illustrate those environmental variables that negatively affect forest primary production (Vitousek, *et al.*, 1988; Flanagan and Johnsen, 1995; Harrington *et al.* 1995; McNulty and Swank, 1995; Zhang and Marshall, 1995; to name but a few). In the following Sections the underlying theory of carbon isotope fractionation in C_3 plants and relevant measurement techniques are briefly presented.

1.6.3.1 Carbon isotope analysis

Theory

There are two naturaly occurring stable isotopes of carbon, ^{12}C and ^{13}C. Most of the carbon is ^{12}C (98.9%), with 1.1% being ^{13}C. Plants discriminate against ^{13}C during photosynthesis in a way that reflects plant metabolism and environment (O'Leary, 1981). Because the isotopes are stable, information inherent in the ratio of abundances of carbon isotopes ($R = {}^{13}CO_2/{}^{12}CO_2$), is invariant as long as carbon is not lost (Farquhar *et al.*, 1989). The measurement of natural variations in the concentration of the stable isotopes of the elements that constitute the bulk of organic matter (such as carbon), is assuming increasing importance in biology (Preston, 1992). Since carbon is continually fixed by the leaf, measuring the synthesis of carbon isotope provides a long-term indicator of plant metabolism that takes account of chronic changes of the photosynthetic parameters (Ehleringer *et al.*, 1990). During photosynthetic gas exchange, the stable isotopic ratio, R, of carbon dioxide assimilated, differs from that of the source CO_2 available to plants (Farquhar *et al.*, 1989) and as a result the $^{13}C/^{12}C$ ratios of organic materials are lower than those of atmospheric CO_2 (Stuiver, 1978). There are two primary processes that cause carbon isotope ratios to change during photosynthesis, *i.e.*, diffusional fractionation and enzymatic fractionation (Flanagan and Johnsen, 1995). Carbon dioxide molecules

containing ^{12}C are lighter and, therefore, diffuse into the leaf at a faster rate (by a factor of 1.0044, or 4.4‰) than CO_2 molecules containing ^{13}C (Craig, 1954 cited in Flanagan and Johnsen, 1995). The basis of the biochemical discrimination against ^{13}C in C_3 plants lies with the primary carboxylating enzyme, ribulose-1,5-bisphosphate (RuP_2C) carboxylase (Farquhar *et al.*, 1982) which preferentially uses $^{12}CO_2$ (by a factor of 1.029, or 29‰) and so discriminates against $^{13}CO_2$ (Roeske and O'Leary, 1984). However, when stomata close and the intercellular CO_2 supply is limited, the stable isotopic carbon ratio in plant material increases as proportionally more ^{13}C is incorporated into photosynthate (McNulty and Swank, 1995).

Carbon isotope measurements

The absolute isotopic composition of a sample, R, is not easy to measure directly (O'Leary, 1981). Rather, the mass spectrometer measures the deviation of the isotopic composition of the material from a standard, $\delta = (R-R_s)/R_s = R/R_s-1$ where R_s is the molar abundance ratio $^{13}C/^{12}C$ of the standard carbon in carbon dioxide generated from a fossil belemnite from the Pee Dee Formation, denoted PDB, for which $R_s = 0.01124$ (Farquhar *et al.*, 1982). Organic matter is invariably depleted in ^{13}C compared to PDB, so R values of organic materials are negative (O'Leary, 1981). Carbon isotope discrimination values, Δ, reflect a difference in isotopic composition between source and product of carbon (O'Leary, 1981) and it is calculated as shown below (Farquhar *et al.*, 1982):

$$\Delta = (\delta_a-\delta_p)/(1+\delta_p)$$

where δ_a is the $\delta = R_a/R_s-1$ value for source atmospheric CO_2 (-0.0079; Flanagan and Johnsen, 1995) and δ_p is the $\delta = R_p/R_s-1$ value for plant tissue.

Carbon isotope discrimination, Δ, is independent of the isotopic composition of the standard used for measurement of δ_a and δ_p and plants show a positive discrimination

against ^{13}C (Farquhar *et al.*, 1982). Farquhar *et al.* (1982) also derived the following expression for C_3-plants:

$$\delta_p \cong \delta_a - u - (v - u)c_i/c_a$$

where c_i and c_a are the CO_2 concentrations in the leaf intercellular spaces and external atmosphere surrounding the leaf, respectively. As explained above, u = 4.4‰ (discrimination by the diffusion through the stomatal pores) and v = 29‰ (discrimination by the RuP_2 carboxylase).

Variables that reduce CO_2 assimilation rate through effects on capacity for photosynthesis (for example very low photon flux densities, and deficiencies of certain mineral nutrients) will increase c_i/c_a and reduce δ_p. So, if $\delta\,^{13}C$ becomes less negative at constant c_a and constant $\delta\,^{13}C$ of CO_2 in the air, decreased c_i is indicated (Martin and Sutherland, 1990). A less negative value of $\delta\,^{13}C$ indicates tissue richer in ^{13}C or 'heavier' (O'Leary, 1981). However, the interaction of the variables that determine c_i is complex. A change in environmental conditions may have no effect on c_i and δ_p, if the resulting shifts in stomatal and carboxylation resistances are in the same direction and of similar size (Saurer *et al.*, 1995). Francey and Farquhar (1982) suggested that nutrient depletion, water stress and light availability are the most important environmental influences acting on the fractionation process in trees, that operate locally but at decadal to century times scales.

Carbon isotope applications

Despite the complexity of the factors driving the variability of $^{13}C/^{12}C$ ratios in plant tissues, researchers have successfully used this method to estimate influences of the environment on trees growing at different sites (Zhang and Marshall, 1995; Harrington *et al.* 1995; Flanagan and Johnsen, 1995; Vitousek, *et al.*, 1988). In addition, Fleck *et al.* (1996) indicated that the parameter Δ is interesting for ecophysiological studies, since it is not only an indicator of long term intercellular

carbon dioxide concentration and thus of water use efficiency in C_3 plants, but also provides a time-integrated measure of plant response to changes in the environment such as water availability (see also Ehleringer and Cooper, 1988). The nutritional status of a plant may also affect the observed isotope discrimination. For example well-nourished plants had less negative $\delta^{13}C$ values than did plants deficient in nitrogen and/or potassium (O'Leary, 1981).

Leavitt and Long (1988), studied pinyon pine (*Pinus edulis*) trees from nine sites in Arizona and estimated that $\delta^{13}C$ was negatively correlated with ring width, while Martin and Sutherland (1990) found reduced ring width for Douglas-fir (*Pseudotsuga menziesii*) in periods with SO_2 emissions from a nearby smelter accompanied by high $\delta^{13}C$ values. Results consistent with the previous investigations were presented by McNulty and Swank (1995) for *Pinus strobus* in which significant relationships between Δ and basal area were detected. The variability of $^{13}C/^{12}C$ ratio in cellulose of tree rings was originally used to reconstruct the time course of $^{13}C/^{12}C$ in atmospheric CO_2 (Tans and Mook, 1980). Soon, it was discovered that isotope fractionation processes correlated with precipitation and temperature and it is feasible to use isotope variations for climatic reconstruction (Leavitt and Long, 1988; Lipp, *et al.*, 1991; Saurer *et al.*, 1995; Saurer *et al.*, 1997). However this approach is not straightforward because several other variables (*e.g.*, site nutrient and water availability) influence the carbon isotope fractionation at the same time (Saurer *et al.*, 1997).

In Chapter 5, an ANPP study made along an elevational gradient in a Mediterranean beech ecosystem will be presented. Analyses of foliar nitrogen concentrations and carbon isotope discrimination were made to gain insight into the environmental factors that may constrain productivity at different elevations. In the following Section, a brief presentation of the ecology and the evolution of *Fagus* is given.

1.7 THE STUDY SPECIES

1.7.1 Taxonomy and morphology of *Fagus*

The word *Fagus* originates from the Greek language (meaning edible) and this name was given to the genus by Linnaeus in 1735. The genus *Fagus* belongs to *Fagaceae* family (subfamily *Fagoideae*) and is considered to be a morphologically homogenous genus (Peters, 1997), with tall monoecious deciduous trees. The buds are spindle-shaped (fusiform), pointed and rather large and the flowers are anemophilous. The male flowers are in pendulous clusters with 8-16 stamens while the female flowers are usually in pairs, surrounded by a stipitate, scaly cupule which becomes woody in fruit. The number of styles is three (Tutin *et al.*, 1964). The fruits are a four parted cupule which includes two triangular nuts. On germinating, these have two large, rather kidney-shaped, cotyledons.

Shen (1992) classifies 13 species in the *Fagus* genus and their distribution is depicted in Table 1.1. The vast majority of the species is encountered in east Asia, and only one is found in N. America and one in Europe. However, Strid and Tan (1997) distinguish the Greek material of *F. sylvatica* L. into two subspecies; *F. sylvatica* subsp. *sylvatica* (European beech) which is a strictly montane species of the Mediterranean basin and *F. sylvatica* subsp. *orientalis* (Oriental beech) which is distributed in west Turkey, Romania, Bulgaria and north-eastern Greece. *F. sylvatica* is a deciduous tree 20-35 m in high with a bole diameter up to 1.8 m and a conic crown in youth, becoming domed on radiating branches in open-grown old trees (Figure 1.1). Forest-grown trees have narrower crowns and long straight boles. The bark is smooth, silvery grey, only slightly roughened in old trees, rarely becoming somewhat scaly and platy. The shoots are green-brown and covered with silky hair at first, usually zig-zagged from node to node, becoming dull purple-brown, hairless with oval buff lenticels. The buds are spindle-shaped, sharp pointed, light brown and *ca* 1-2 cm long. The leaves are oval to obovate, with acute apex, wedge-shaped base and five to seven pairs of veins. The upper surface soon hairless, with light green medium to dark green colour, while the underside is light green, with slightly raised

Table 1.1: Taxonomy and distribution of *Fagus* genus according to Shen (1992).

Species	Distribution
F. japonica	Japan
F. okamotoi	Japan
F. crenata	Japan
F. engleriana	China
subsp. *multinervis*	S. Korea
F. brevipetiolata	China
F. tientaiensis	China
F. bijiensis	China
F. lucida	China
F. chientii	China
F. hayatae	Taiwan
subsp. *pashanica*	China
F. longipetiolata	China
F. grandifolia	N. America
subsp. *mexicana*	Mexico
F. sylvatica	Europe
subsp. *orientalis*	West Asia

Figure 1.1: Open-grown beech tree (*F. moesiaca*) growing in north-central Greece (photo K. Bidakis).

veins which are hairy especially in the axils. Their margin is wavy, with autumn colour yellow to orange-brown (Rushforth, 1999). According to Strid and Tan (1997) subspecies *sylvatica* has 6 - 8 pairs of lateral veins (subsp. *orientalis* with 8 - 12 pairs), and the fruiting peduncle is *ca.* 15 mm (*ca* 50 mm in subsp. *orientalis*). Flowering takes place in May and early June. The male flower comprises a small, hairy, four-lobed greenish calyx with numerous yellow stamens which form a round, bobble-like catkin hanging from a long stalk with two small stipules. The female flowers are green, on a stiff hairy stalk, in the axils of the upper leafs on current season's shoots (Figure 1.2). During the summer the cupules expand, become hard and woody, and develop soft brown spines as well as a stalk having similar length to the cupule. When mature, they split at the top revealing 1-2 beechnuts within (Sfikas, 1978). The fruit comprises a woody cupule up to 2 cm in length on a hairy 1 cm stalk, that opens along four sutures, with the outer surface hairy and with spaced reflexed linear- pointed prickels. The nutlets within are in pairs of triangular shape in section (Rushforth, 1999). The fruits have a restricted capacity for dispersal and their

Figure 1.2: Male (left) and female (right) flowers of *F. moesiaca* trees (photo K. Bidakis).

germination potential decreases rapidly with age, so that the trees spread slowly (Heywood, 1993). Strid and Tan (1997) support the view that *F. sylvatica* subsp. *sylvatica* and *F. sylvatica* subsp. *orientalis* are typical geographical races of *F. sylvatica* and several individuals have been recorded to be more or less intermediate between these subspecies. Such hybrids are referred to as *F. sylvatica* subsp. *moesiaca* with 5-9 pairs of lateral veins and often somewhat spathulate basal cupule scales. However, Tutin *et al.* (1964) supported the that *F. moesiaca* (K. Maly) Czecz, is a variant between subsp. *sylvatica* and subsp. *orientalis* while Rushforth (1999) distinguished *F. moesiaca* as a different species, having narrower and more wedge-shaped leaves with more veins than *F. sylvatica*, but with the cupule bearing longer and softer prickles. Most Greek beeches, are said to belong to the Moesian beech

type which is highly variable but generally are most similar to European beech (Bergmeier and Dimopoulos, 2001). Dafis (1969) reported that the prevalent beech species in central and north west Greece is *F. moesiaca* and he further identified two forms namely *spatulolepsis* and *tainiolepsis*.

1.7.2 Occurrence and ecology of *Fagus*

Peters (1997) reports that the genus *Fagus* appears to be rather homogenous at the world-wide scale. He also points out that, most likely, the origin of *Fagus* is to be located in east Asia and that the spread of the species over northern latitudes took place during the early Tertiary. Lower temperatures during the Pliocene forced beech species to move southwards in Europe while the interchange between cold and warmer periods in the Quaternary greatly influenced the geographical boundaries of *Fagus* (Peters, 1997). After the last Pleistocene glaciation, the species spread north again from the Balkans which are regarded as its main glacial refuge in Europe (Huntley and Birks, 1983). They also reported that *Fagus sylvatica* expanded about 1200 km between 9000 and 4000 years B.P and nowadays mono-dominance of *Fagus* throughout Europe is ascribed to forest-use and species-favouritism during the early Holocene.

Demesure *et al.* (1996) reported that the fossil pollen data indicate two main refugia in the south of Europe: Calabria (Italy) and the Carpathes. According to Demesure *et al.* (1996), the recolonisation (during the early postglacial) of Europe had its origin in the Carpathian refuge. The beeches coming from the south of Italy seemed to be stopped by the very rapid progression of those originating from the Carpathes. Table 1.2 summarises the history of the genus during different geological periods across the globe from fossil records and Peters (1997) presents a rather extensive analysis of the evolution of this species. Nowadays, beeches are distributed over a large geographical area (37° N to 60° N) from North America south into Mexico; in eastern Asia the species can be found in China, Japan, Korea, Taiwan and into northern Vietnam. It is widespread in Europe from southern Sweden and England in the North, to the Balkans, Italy, Spain, Turkey and the Caucasus to the South.

Table 1.2: Records of fossil findings (as modified by Peters, 1997).

Period	Epoch	B.P. (million yrs)	Records
Cretaceous		135-63	*Nothofagus* pollen records in south Australia and Argentina.
Tertiary	Palaeocene	63-58	*Fagus* in northern and eastern China.
	Eocene	58-36	
	Oligocene	36-25	Fossil *Fagus* pollen in Canada; Oldest fossil leaves in Europe.
	Miocene	25-13	*Fagus* pollen in Europe. First occurrence of *Fagus* in Mexico and Japan.
	Pliocene	13-2.5	*Fagus* retreats south.
Quaternary	Pleistocene	2.5-0.01	Repeated northward spreads and southward retreats of *Fagus*.
	Holocene	0.01-present	*Fagus* spreads north

1.7.3 Distribution in Greece

Most present-day Greek *Fagus* forests established 2000-6000 years B.P (Bergmeier and Dimopoulos, 2001) and nowadays they occupy about 10% of the total Greek forested area, since they are encountered only in the northern and central parts of the country. They are found in all principal mountain areas above 800 m altitude on the northern Greek mainland with the southernmost limit in mountain Oxia (38° 46'N) - the Greek word for beech – located in central Greece. Beech trees make up either pure or mixed stands (mainly with *Abies*) in the cloud belt at *ca* 800 - 1700 m, usually forming the treeline at about 1900 m on many mountains but are scattered in the southernmost part of the range. The species is rarely found below to 200 m or above to *ca* 2000 m elevation, *i.e.,*. mount Olympus (Strid and Tan, 1991). Generally, *Fagus sylvatica* is found in the central, north-central, and north-west Greece, at high elevations, while *Fagus orientalis* spreads to eastern Greek Macedonia at moderate altitudes. *Fagus moesiaca* trees tend to grow at relatively low altitudes (300 - 1000 m) in central and north-west Greece (Karagiannakidou, 1993).

Dafis (1969) vertically distinguished beech forests in Greece into the following three types, according to the characteristic species: *Fagetum submontanum* (900 - 950 m, *Fagus orientalis* or *Fagus moesiaca* f. *spatulolepis*), *Fagetum montanum* (900 - 1600 m, *Fagus moesiaca* f. *tainiolepis*), and *Fagetum subalpinum* (1600 - 1800 m, *Fagus moesiaca* or *Fagus sylvatica*). However, it would be unrealistic to draw a characteristic line demarking the horizontal and vertical distribution of the three species or subspecies, since a broad range of intermediates occur in the contact areas. Smyris (1980, cited by Karagiannakidou, 1993) reported that in the Voras mountain - the physical boundary between Greece and Macedonia - the most prevalent species is *Fagus sylvatica* while Dafis (1969) indicated that the main species encountered in central and north west Greece is *Fagus moesiaca*. Karagiannakidou (1993), who investigated beech forests on Chortiatis mountain (located in the Chalkidiki peninsula), reported that Moesian beech were also found in this part of northern Greece. Recently, a more detailed study by Bergmeier and Dimopoulos (2001), and

based mainly on species composition, indicated that the following five vegetation groups are present in the Greek beech forest communities.

1) Humid mesotrophic habitats which include, **i)** *Geranium versicolor – Utrica dioica – Fagus sylvatica*, **ii)** *Galium odoratum – Fagus sylvatica,* **iii)** *Lamiastro montani – Fagetum sylvaticae,* and **iv)** *Soldanello rhodopaeae - Fagetum sylvaticae* vegetation types.

2) Acidic habitats with only one community *viz. Orthilio secundae- Fagetum.*

3) Calcareous high–altitude habitats including two associations, **i)** *Geranium macrorrhizum – Fagus sylvatica,* and **ii)** *Cardamine graeca – Fagus sylvatica.*

4) Moderately warm and dry habitats with, **i)** *Lathyro alpestris – Fagetum sylvaticae,* **ii)** *Geranio striati – Fagetum,* and **iii)** *Rubus canescens – Fagus sylvatica* vegetation types.

5) Warm to dry habitats at low to medium altitudes described by *Fagus sylvatica* ssp. *orientalis* community.

1.7.4. Ecology of *Fagus*

Beech trees are very shade tolerant during their youth, with straight tall stems (25 m) that cast deep shade, adapted to both acidic sands and chalk or limestone downland. They need freely drained soils, and do not tolerate waterlogging at the roots (Rushforth, 1999). Over-exploitation has caused severe deterioration of Mediterranean forests, and Greek beech ecosystems have suffered from grazing, cutting, and burning. However, nowadays most *Fagus* woodlands are naturally regenerating, and some remote stands have not been disturbed for many decades.

Bergmeir and Dimopoulos (2001) reported that in their general appearance, Greek beech forests are similar to Central European forests with floristic and ecological

parallels throughout Europe. They finally concluded that in Greece, a wide range of habitats permits natural *Fagus* forests to thrive, and a remarkable diversity of beech - dominated communities still exists.

1.8 STRUCTURE OF THE THESIS

This Thesis consists of two main parts: the theoretical (Chapter 2 and Chapter 3) and the other empirical (Chapter 4 and Chapter 5).

In Chapter 1 the basic concepts and ideas that are used in the following Chapters have been introduced. In particular, theoretical and statistical aspects of allometric relationships broadly applied in plant science were briefly presented. In addition, the general topic of fractal geometry in the context of forest research has been introduced, and an epigrammatic account of forest biomass studies has been outlined. A European database for stem volume and biomass functions of major tree species is also introduced in this part. The compiled equations are available in a digital format on a disc at the back cover of the Thesis. Concepts, definitions and methodological aspects of estimating ANPP are also summarised in Chapter 1, while theoretical principles and applications of carbon isotope analysis in productivity studies are presented. Finally, the evolution, the ecology and the occurrence of the study species (*Fagus sylvatica* Cz.) were briefly reported.

Chapter 2 introduces a biomechanical model and a reductionist approach based on fractal geometry. The biomechanical model explains a large part of the variability in the allometric parameters obtained when aboveground tree biomass is regressed against diameter at breast height (see Eq. 1.1) for different tree species growing across the globe. The model is formulated within the context of the principles provided by engineering theory, and adjusted to take into account a mathematical artefact that partly contributes to the covariance exhibited by the allometric parameters a and b. The reductionist model treats individual trees as fractal objects

and an approach that demonstrates the underlying relationships between the different variables describing tree size-shape allometry is presented.

In Chapter 3, simplification methods of allometric analysis for estimating forest biomass are presented. Moreover, a new straightforward method for determining standing biomass is developed and is totally based on a global meta-database and statistical assumptions made by allometric relationships. The new approach (called SSS), predicts the aboveground biomass by harvesting the smallest (no less than 2 cm in *D*) trees in the stand. Validation against ten independent data-sets gave quite good results.

In Chapter 4, empirical allometric relationships for several dendrometric characteristics of *F. moesiaca* the study species in Vermio Mountain, Northern Greece, are developed. The models are applied to the beech stands and resulting estimates of ANPP are reported in Chapter 5. Growth efficiency, leaf area index, and biomass of different tree compartments at the stand level are also determined. Carbon isotope analysis and foliar nitrogen concentration from harvested trees are used to gain insight into the environmental variables that may limit productivity along an elevational gradient in this ecosystem. Finally, a general discussion about the work previously presented is given in Chapter 6.

2. BIOLOGICAL INTERPRETATION OF TREE SIZE-BIOMASS ALLOMETRY

2.1 INTRODUCTION

Life reflects the way different levels of organisation in individuals are integrated through correlations among size, shape, structure, chemical compositions and other biological processes. Terrestrial plants span an enormous range of size while a single *Sequoia* tree functions across eight orders of magnitude in body size as it develops from seedling to adult tree. As the size of an organism changes, the relationships among its different components and processes must be adjusted so that the organism can continue to function. Galileo Galilei (cited in Niklas, 1994) argued that shape must change among related organisms differing in size whenever geometrical similarity is required.

The first and most familiar way in which size change affects shape is by simple allometry; that is, as an organism get smaller or larger, its proportions will retain a constant scaling relationship. Theoretical studies about allometric equations commonly found in variables describing tree size-shape relationships can fall into three major themes. The first is derived from Leonardo da Vinci's observation that 'All the branches of a tree at every stage of its height when put together are equal in thickness to the trunk (below them). All the branches of a water (course) at every stage of its course, if they are of equal rapidity, are equal to the body of the main stream.' (Leonardo's note No. 394, translated by Richter 1970). Motivated by this remark, Shinozaki *et al.* (1964a; 1964b), observed that foliage weight and sapwood conducting area in the crown were linearly related, and subsequently developed the pipe model theory, which suggested that a given unit of transpiring foliage is supplied with water by a corresponding unit of conducting sapwood.

The second theme has initiated from the inquiries on the ability of tall trees (more than 100 m) to transport water and nutrients to such heights. These studies mainly focus on the hydraulic architecture of plants and try to understand the physical and biological processes which govern the flow of fluid within the vascular system (Zimmermann, 1978). Thus, resistance-conductance models have been proposed to show how water potential gradients are influenced by several anatomical, physiological, and environmental factors. This approach tends to ignore the complex dynamics of fluid flow through the vascular tubes and modelling is based on the analogies to electrical circuits (Mencuccini and Grace, 1996).

Last but not least, mathematical and mechanical principles have also been implemented to understand plant form and architecture through the physiological requirements to conserve water and to support large loadings against the influence of gravity and/or wind forces. These studies mainly use fractal geometry in response to plant optimisation of sunlight, water, or nutrient resources by leaves, branches, and roots (Berezovskava *et al.*, 1997), to resist buckling resulting from wind and gravity (McMahon, 1973), and to obey other biomechanical principles (Niklas, 1992). Recently, West *et al.* (1999), integrated the aforementioned themes, and developed a model (hereafter WBE model) that predicts several structural plant variables (stem diameter, number of leaves and branches, tree height, *etc.*) in relation to plant body size.

In this chapter the following objectives have been set:
(i) To test the performance of the WBE model which relates aboveground tree biomass (M) to diameter at breast height aboveground (D),
(ii) to propose and validate a biomechanical model which describes the variability of coefficients found in stem biomass M_S-D relationships,
(iii) to derive analytically a 'reductionist' model demonstrating the underlying relationships between the variables describing tree size and shape based on principles and ideas provided from fractal geometry,

(iv) to assess the usefulness of different models in predicting aboveground tree biomass and finally,
(v) to illustrate phylogenetic differences of the *M-D* equation of forest trees.

2.2. THEORETICAL MODELS OF TREE SIZE-BIOMASS ALLOMETRY

2.2.1. Allometric relationships

In the biological sciences, the study of size-correlated relationships in organic form and process is called allometry, meaning cross-measurement and dates back from work by Huxley (1924, 1932) who coined the term, and Thompson (1917) who produced synthetic works on scaling in biology. Gould (1966) suggested that changes in size and shape relationships in individuals with time be termed *growth allometry*, whereas studies involving different individuals be termed *size allometry*. White and Gould (1965) proposed that allometric relationships which occur among adults of related species, genera, families, *etc.*, be termed *allomorphosis*. The definition of the simple allometric hypothesis specifies proportionality between the relative growth rates of two size variables and implies that related changes are maintained constant through ontogenesis.

According to Niklas (1994), allometry, in its general use, has three meanings:

- the growth of a part of an organism in relation to the growth of the whole organism or some part of it,
- the study of the consequences of size on form and process, and
- to connote departure from geometric similitude, which results when geometry and shape are conserved among a series of objects differing in size.

Brown *et al.* (2000) define three different levels of allometric studies in biology: within individual organisms, among different individual organisms of varying size, and within assemblages of multiple individuals or species of organisms. The analysis of this Chapter will be based on data that fall in the last two categories. Foresters and ecologists have applied different scaling equations for estimating forest biomass, but

undoubtedly, the most commonly used mathematical model for biomass allometric studies takes the form of the power function

$$Y = aX^b \qquad \text{Eq. (2.1)}$$

where a and b are the scaling parameters that vary with the variables and the kind of organism under investigation; Y is the total or the component biomass and X a tree dimension variable (*i.e.* D, D^2, D^2H, DH, *etc*). In the case of $b = 1$, Y and X are isometrically related.

Kittredge (1944) is thought to be the first who introduced the allometric function into quantitative forest ecology. He used empirical data to calibrate the power model (Eq. 2.1) for estimating foliage weight per tree from the diameter at breast height. Power functions for biomass studies have been used world-wide and it is unquestionable that researchers have produced a voluminous amount of allometric relationships for several species and tree components. Thus, the estimation of tree total aboveground biomass (M) is often related to diameter at breast height (D) and in most cases the R^2 in this relationship is above 90%.

Although some studies have also used tree height H, in conjunction with D, the slight increase in predictability of such regressions over those using diameter alone is probably not practical with regard to accuracy of height measurements (Peterson *et al.*, 1970; Crow, 1971; Schmitt and Grigal, 1981; Harding and Grigal, 1985, to name but a few). The standard method to obtain estimates for the coefficients a and b is by the least square regression of log-transformed data for M and D measured from destructively sampled trees that represent the diameter range of the stand under investigation. We now turn our discussion to the biomechanical principles applied to tree shape-size relations where extensive use of allometry is being reported.

2.2.2 Theoretical aspects of biomechanical models

Values of a and b in M-D allometric equations are considered to vary with species, stand age, site quality, climate, and stocking density of stands. Baskerville (1965) developed allometric relationships for balsam fir (*Abies balsamea* M.) based on sampled trees selected from plots with different stocking density. He concluded that stocking density had no significant effect on the allometric equations that relate M to D and a single expression was developed for all trees regardless of stocking density. The same conclusion can also be drawn from Bartelink (1996 and 1997) who built total aboveground and stem biomass equations for Douglas fir, and beech trees in the Netherlands, based on individuals that originated from stands of different age.

Recently, Martin *et al.* (1998) destructively harvested 87 trees made up of 10 deciduous species growing in the Coweeta Hydrological Laboratory in western North Carolina in order to derive interspecies pooled equations. The regressions obtained gave quite accurate predictions for the biomass values of different tree components (stem, foliage, branch and the total aboveground biomass). Thus, there is some evidence that stand structure and tree phylogeny may not necessarily play a significant role in the shape of the M-D relationship. The study of the interplay between stem volume (V_S), stem dry biomass (M_S), D, and H through engineering principles was initiated with Greenhills' (1881) analysis on the mechanical stability of a vertical column to resist collapse under its own weight. He considered both the case where the tree is a uniform cylindrical pole and where the stem tapers to a point. The maximum height (H_{cr}) of the column is given by the Euler-Greenhill equation

$$H_{cr} = C(E/\rho)^{1/3}D^{2/3} \qquad \text{Eq. (2.2)}$$

where C is the constant of proportionality, E denotes Young's elastic modulus and ρ is the stem density. However, this model overestimates critical heights since the mass of the branch and foliage was not taken into account. King and Loucks (1978) outlined a more realistic approach by modelling the crown mass to act as a point load atop a trunk and located it at the crown centre. According to their model, the value of

C depends on the ratio of crown to stem biomass. However, both crown/stem biomass and tree height were held constant in calculating the critical diameter and therefore the critical dimensions were overestimated (Holbrook and Putz, 1989; Niklas, 1992). Another theoretical approach was reported by Gere and Carter (1963; cited by Holbrook and Putz, 1989 and Niklas, 1992), whose formula relates H_{cr} to the ratio of the diameter at tree base to the diameter at the crown centre of mass. More recently, Holbrook and Putz (1989) attacked the problem of buckling dimensions by applying the theory of virtual work which states that for a body to be in elastic equilibrium, the total work done on it by external forces must equal the increase in elastic energy, stored within the body.

Apart from biomechanical constraints applied to the stature that a tree can attain, biological processes also play an important role in this respect. For example, a biological trade-off between acquisition of light and elastic buckling is a likely explanation for tree height (Kuppers, 1989). According to Givnish (1982), the success of terrestrial plants to survive and reproduce is partially governed by their ability to grow taller. Photosynthetic units of tall trees are located above their neighbours, with the advantage of intercepting larger quantities of light, and providing better access to pollinators and dispersal agents (Niklas, 1992). However, as more assimilates are allocated to primary growth, the risk of mechanical failure is higher since the stem cannot support the biomass of the tree, and/or resist additional dynamic forces (induced by wind pressure and snow accumulation). At this point it should be mentioned that hydraulic limitations also play an important role in determining tree height (Magnani *et al. submitted*) .

The mechanical design of trees (in terms of *H-D* relationships) has been studied using three different models, derived from engineering first principles. The first one is termed geometric self-similarity, and supports that an isometric relationship exists between tree diameter and height. King and Loucks (1978) reported that this type of design is the most effective in resisting wind pressure. On the other hand, the elastic similarity model ($H \propto D^{2/3}$) produces a uniform deflection of the stem responding to

self-loading (Eq. 2.2). The third approach, the stress similarity model, assumes that a constant maximum stress is maintained through the length of a branch or a tree trunk and predicts that $H \propto D^{1/2}$ (McMahon, 1973; McMahon and Kronauer, 1976; Niklas, 1994). Assuming a constant stem wood density and based on dimensional analysis, predictions for scaling relationships between V_S, M_S, D, and H, in terms of the aforementioned models, are readily obtained. For example, the geometric similitude predicts that $M_S \propto V_S \propto D^2H \propto D^2D^1 \propto D^3$ while predictions from the elastic and stress model are presented in the following Table.

Table 2.1: Predictions for scaling exponents in *H-D* and M_S *-D* relations from three different models. b^* denotes the scaling exponent in *H-D* allometry and d^* denotes the scaling exponent in M_S –D allometry.

	Geometric model	*Elastic model*	*Stress model*
$H \propto D^{b^*}$	$b^* = 1$	$b^* = 2/3 \sim 0.67$	$b^* = 1/2 = 0.5$
$M_S \propto D^{d^*}$	$d^* = 3$	$d^* = 8/6 \sim 2.67$	$d^* = 5/2 = 2.5$

McMahon (1973), advanced the analysis made by Greenhill (1881), and calculated the height above which a tree is likely to suffer elastic collapse (H_{cr}), for a given diameter. He plotted log$H$ against log$D$ for very large trees and a slope of 2/3 was obtained. Thus, he concluded that adaptation to elastic reaction against wind forces may explain the stature of big trees and the critical buckling height was computed as $H_{cr} = 4.3D^{2/3}$, when height and diameter are expressed in metres. Furthermore, he reported that H of very large trees is about 1/4 the critical height (H_{cr}). However, the value of 2/3 is hardly surprising since the critical height was calculated with Eq. 2.3, assuming that E/ρ is constant for different trees and C equals to 0.792.

Niklas (1994), questioned the methodology used to derive the theoretical H_{cr} and computed the critical height totally based on empirical values of E and ρ available for 56 trees belonging to 56 species and setting $C = 0.792$. The regression line obtained with the least square method gave $H_{cr} = 97.7D^{0.689}$ when both dimensions are in metres. The safety factor $S = H_{cr}/H$ for the analysed data equalled 4.74, *i.e.*, slightly

larger than the value of 4.0 that was reported in McMahon (1973). Niklas (1994), computed the confidence interval of the reduced major axis scaling exponent and found that it fell between 0.66-0.74, indicating that the critical height roughly scales as the 2/3 power of stem diameter.

Niklas (1994) also supported (based on several *H-D* studies) the view that a single model could not explain the allometric relationship between the *H-D* variables and proposed that geometric similitude may describe the allometry in young trees, while the elastic and the stress similarity models are more appropriate during the adult and mature stages of ontogenesis, respectively. To verify this speculation, he presented in a subsequent article, tree scale data for *Robinia pseudoacacia* trees which ranged from less than 1 mm to about 2 m in diameter (see Figure 3 in Niklas, 1999). Indeed the shape of the scaling regression changes during ontogenesis – as indicated by the scaling exponent - but no inferences were made about the scaling constant.

So far, analysis on the allometry of the variables describing tree size-shape relationships have been based exclusively on the allometric exponent, implying that the scaling constant is of little biological significance, if at all. However, it is expected that a negative autocorrelation between the values of scaling parameters in the *H-D* relation and in effect in M_S-*D* allometries (according to Table 2.1) should exist if trees are to resist dynamic and static forces. Contrary to plant biologists, zoologists have thoroughly studied the correlation of the coefficients found in the allometric equations describing the relationship between the size of different organs in mammals and other species (Hersh, 1934; White and Gould, 1965; Gould, 1971; Pagel and Harvey, 1988). White and Gould (1965) concluded that, when *b* varies, no biological interpretation could be deduced from this relationship. They pointed out that the self-correlation of *a* and *b* simply arises from the choice of measurement units, the algebraic equation itself and the limited field (*a, b*) of the collected values. An inherent mathematical artifact was considered to be the only reason for the observed relationship between *a* and *b*, in zoological studies (Lumer, 1936; White and Gould, 1965; Gould, 1971). However, Lumer (1936) concluded that the

biological significance of this relationship is important but no study has been conducted so far to investigate further this problem.

In the following paragraphs a biomechanical model, which predicts the relationship between the scaling coefficients in M_S-D, is formulated. The diameter was selected as the independent variable related to tree size and age (larger and older trees have bigger D) and the M_S-D relation was chosen since the coefficient of determination is always higher than in H-D allometries. Thus, statistically biased results in terms of predictions through scaling equations are minimised if M_S-D equations are used. It is also shown that, once the mathematical artifact behind the a-b relationship is accounted for (White and Gould, 1965), there remains a highly important biological significance to be explained.

2.2.2.1 Development of a biomechanical model

Foresters model stem volume according to the formula $V_S = (fD^2H)\pi/4$, where f is a coefficient, called form factor, which is employed to reduce the volume of a cylinder (with linear dimensions equal to D and H) to that of the stem (Philip, 1994). Assuming a constant wood density (ρ) across the trunk, stem biomass is readily computed $M_S = \rho V_S = \rho(fD^2H)\pi/4$. Considering critical buckling height (H_{cr}), the critical stem biomass is therefore given as $M_{Scr} = p(fD^2H_{cr})\pi/4$ and since $H_{cr} = a_{cr}D^{Bcr}$, substituting in the last equation results in:

$$M_{Scr} = KD^{2+Bcr} \qquad \text{Eq. (2.3a)}$$

where $K = \rho f a_{cr}\pi/4$. On the other hand, Enquist *et al* (2000) have demonstrated that M_S-D relationship conform to the power model:

$$M_S = a^*D^{d^*} \qquad \text{Eq. (2.3b)}$$

where a^*, d^* are the scaling parameters. By definition (Niklas, 1999), the mechanical safety factor is written as:

$$S = M_{Scr}/M_S \qquad \text{Eq. (2.3c)}$$

and thus substituting Eq.(2.3a) and Eq.(2.3b) into Eq.(2.3c) gives

$S = (K/a^*)D^{2+Bcr-d^*}$ and solving for a^* we obtain

$$a^* = (K/S)D^{2+Bcr-d^*} \qquad \text{Eq. (2.4a)}$$

where the relationship between the scaling coefficients in M_S-D equation is depicted. According to Eq. 2.4a, the relationship between a^*-d^* depends on the D (*i.e.*, on the age or size) of the trees under investigation and this is in accordance with biological interpretation (Niklas 1994; Niklas 1999) and statistical properties of scaling relations (the shape of the allometric regression depends on the interval of the independent variable). In addition to the theoretical derivation of the model, a factor related to the mathematical artifact inherent in the a^*-d^* relationship should also be taken into account. This artifact originates from the fact that the a^*-d^* regression depends on the choice of units of the independent variable (in this case, diameter at breast height). As is illustrated in Figure 2.1, the value of the slope (d^*) remains constant but the intercept (a^*) changes according to the units of measurements of the independent variable (D).

In Figure 2.1A, the slope and the intercept for the equation represented by the black circles, are equal to 2.5 and 7000, respectively. In Figure 2.1B, the same equation has a slope of 2.5 but the intercept has changed to 0.07. The same holds true for any equation and we can conclude that the units of measurement for D play a significant role in the relationship between the allometric coefficients. For example, in Figure 2.1A, the slopes of the two equations are negatively related to the intercepts but this relationship vanishes in Figure 2.1B, since the equations still have very different slopes but their intercepts are now quite similar.

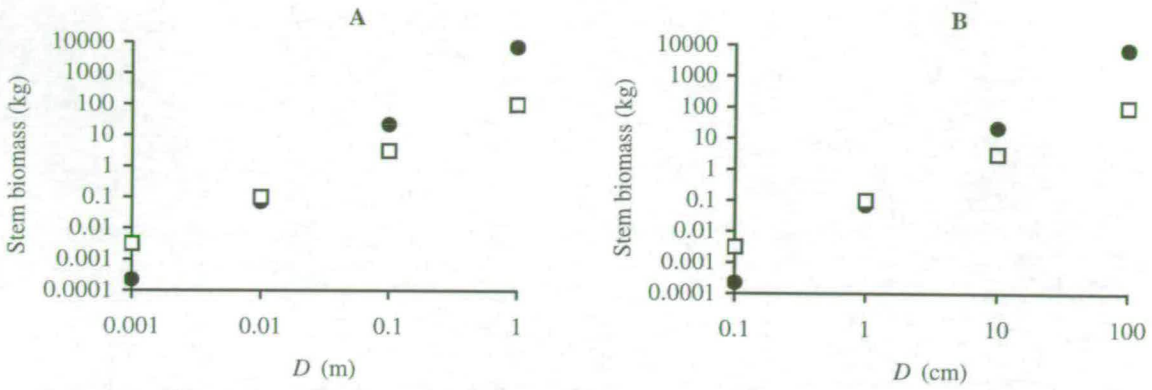

Figure 2.1: Data points for two allometric equations with different values of coefficients. The equation represented by the black circles has a larger slope (d^*), but smaller intercept (a^*) than the equation represented by the open squares. In the left panel (**A**), the diameter is expressed in metres, while in the right panel (**B**), the diameter is expressed in centimetres. Accordingly, the slopes of the two equations remain the same but the intercepts (at D = 1 m or D = 1 cm) depend on the measurement units.

Empirical values of a^* and d^* compiled by Ter-Mikaelian and Korzukhin (1997) were used to illustrate the dependency of a^* on the units of D. This mathematical artefact affects the a^*-d^* relationship. It is worth noting that the coefficient of determination also changes when the diameter is measured in different units (see Figure 2.2). For example, a very strong negative relationship between the allometric coefficients exists when D is expressed in millimetres (Figure 2.2A), but a very weak ($R^2 = 0.23$) relation is illustrated when D is expressed in decimetres (Figure 2.2C). The negative relationship is transformed to very high positive one, if D is expressed in metres (see Figure 2.2D). As it has been mentioned, this mathematical artefact should be taken into account for the development of the biomechanical model.

The mathematical expression that transforms the value of the intercepts, according to the units of the independent variable, takes the form: $a_2^* = a_1^* z^{d^*}$ where a_2^* and a_1^*

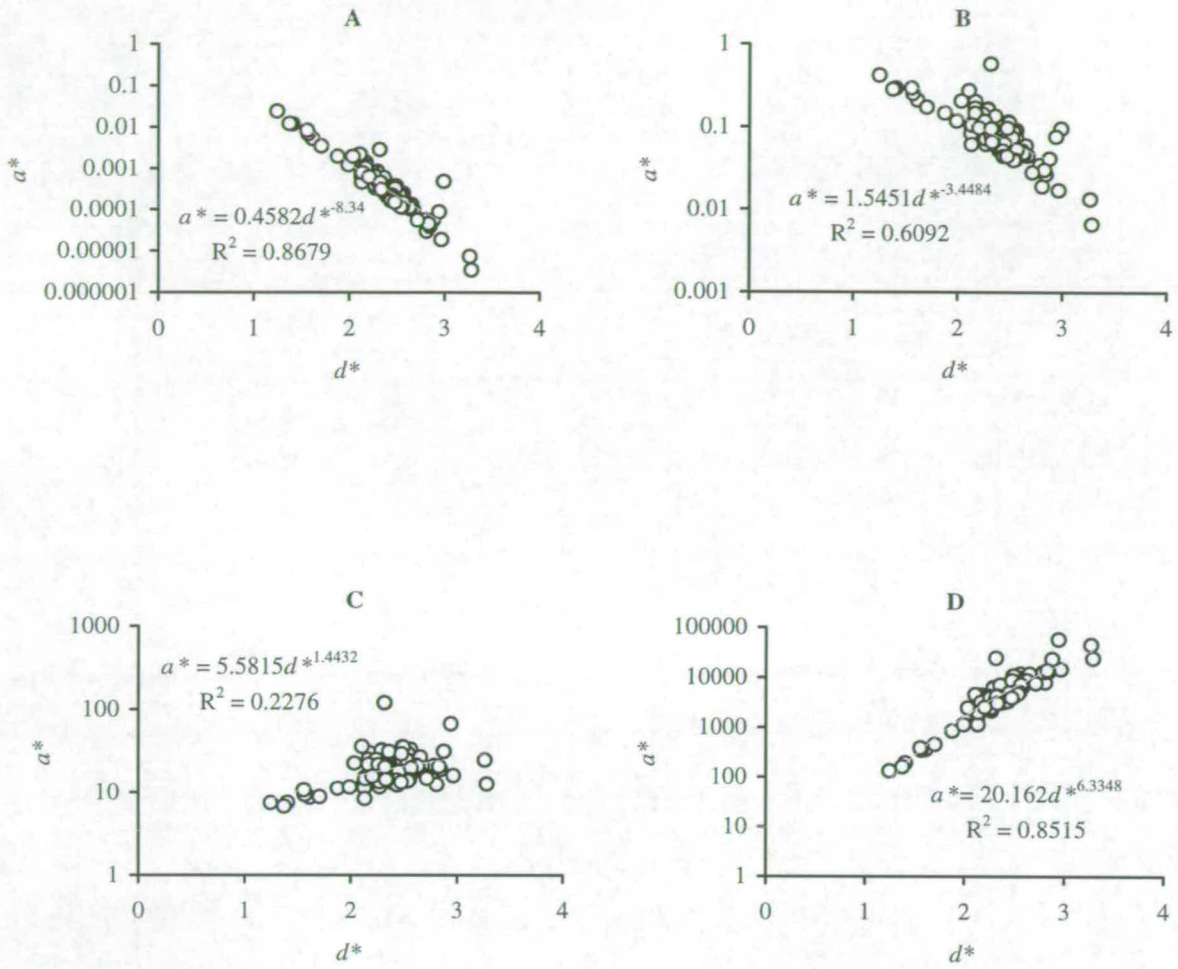

Figure 2.2: The dependency of a^*-d^* relationship on the units of measurements of D. In (**A**) diameter is expressed in mm; in (**B**) diameter is expressed in cm; in (**C**) diameter is expressed in dm and in (**D**) diameter is expressed in m. Apart from the shape of the curve, the coefficient of determination also changes.

are the allometric intercepts for two different units of measurement; the parameter z is a dimensionless number which changes according to the measurement units (see also Niklas 1994, p.23). For example in Figure 2.1B, $a_1^* = 0.07$ for the equation represented by the circles. But, if the D is expressed in meters (Figure 2.1A), then the

intercept changes according to $a_m^* = a_{cm}^* z^{d^*} = 0.07 \times 100^{2.5} = 7000$. To find out the value of the intercept in the millimetre scale then $a_{mm}^* = a_{cm}^* z^{d^*} = 0.07 \times 0.1^{2.5} = 0.000221$, and so on. Incorporating the z^{d^*} parameter in Eq. (2.4a), the biomechanical model reads as

$$a^* = z^{d^*}(K/S)D^{2+Bcr-d^*} \qquad \text{Eq. (2.4b)}$$

and the dependency of the relationship between a^*-d^* on the units of the independent variable is therefore accounted for. We now turn to the second step of the model, estimation of the parameters.

2.2.2.2 Parameterisation of the biomechanical model

Niklas' (1994, p.164) analysis, indicated that $H_{cr} = 409.16D^{0.689}$ when both dimensions are measured in centimetres, and accordingly Eq. (2.3a) transforms to $M_{Scr} = KD^{2.689}$ and Eq.(2.4b) reads as:

$$a^* = 1^{d^*}(K/S)D^{2.689-d^*} \qquad \text{Eq. (2.4c)}$$

At this point it should be mentioned that the critical height could also have been calculated either via Eq. (2.2), or using McMahon's formula, $H_{cr} = 4.3D^{2/3}$. However, since I did not have enough data at my disposal for the density-specific stiffness (E/ρ), equation 2.2 could not be used in the model. In addition, McMahon (1973) derived the aforementioned relationship for H_{cr} from very old specimens, assuming that the E/ρ ratio is constant for different tree species. These assumptions may introduce bias in the predictions of the model and his formula was therefore rejected. The parameter $K = \rho f a_{cr}\pi/4$ depends on the values of wood density (ρ) and form factor (f) and the following assumptions were made for each of them:

i) Stem wood density is supposed to be constant across conifers and broadleaves, and invariant between trees with different ages or between specimens that grow at different sites. This assumption is an over-simplification for real trees, but in the

absence of more detailed information the model was based on this. Data for 56 tree species on wood density are reported in Niklas (1994, Table 3.4) and the average value for ρ (equal to 590.02 x 10^{-6} kg cm^{-3} with a standard deviation of 139.37 x 10^{-6} kg cm^{-3}), was used in the biomechanical model.

ii) The form factor is also reported to vary with stand density, tree species and genotype, tree age, crown size and site factors (Philip, 1994). The assumption that the value of this parameter is also constant for trees with different structural and morphological characteristics was made and a value of 0.5 was selected.

For the scaling constant a_{cr} an empirical value of 409.16 derived from 56 trees had been reported in Niklas (1994, p.164) and was therefore used in the calculation of $K = \rho f a_{cr} \pi/4$ = 590.02 x 10^{-6} x 0.5 x 409.16 x 0.7854 = 0.0948 kg^2cm^{-2}.

The safety factor S was allowed to vary with respect to the size of the tree as indicated in several studies. Trees mechanically perturbed by wind tend to be shorter and to have thicker and more conical stems than trees growing in protected environment (Grace, 1977). For open-grown, very big trees, McMahon (1973) calculated an S of about 4 while for the same specimens, analysis made by Niklas (1994), indicated that the safety factor was about 5. On the contrary, trees when not exposed to winds, and still young, have a safety factor of about 1.5-2 (Speck *et al.*, 1990), while an S range of 1.9-2.7 has been reported for individual *Acer* trees growing in dense stands with D > 18 cm (Sterck and Bongers, 1998, Table 3). Horn (2000), also calculated safety margins for individuals growing in New Jersey (USA) forest, and the reported data were used for the parameterisation of the model. Different values for S, computed as average of the aforementioned studies, are presented in Table 2.2.

However, it should be noted that these values were reported for open-grown trees. On the other hand, individuals growing in cohorts or closed stands tend to approach

Table 2.2: Safety factors (S) for open-grown trees classified according to D. n denotes the number of sample trees. n denotes the number of the sampled trees.

D range (cm)	*S*	*n*	*Source*
0-4	1.75	n/a	Speck et al., 1990
5-9	2.5	37	Horn, 2000
10-22	2.8	98	Sterck and Bongers, 1998; Horn, 2000
23-53	4.7	56	McMahon, 1973; Niklas, 1994
> 53	5	56	McMahon, 1973; Niklas, 1994

critical buckling mass (*i.e.*, attain smaller S values). The reason (according to Holbrook and Putz, 1989) is that, neighbours biomechanically support each other and therefore can elevate higher in the canopy. In addition, the impact of wind forces is reduced within the protected environment of the stand, allowing trees to allocate more biomass to the aboveground parts, rather than to the root system (implying again smaller S).

The compiled safety factors were used in the model since information of S values for stand trees could not be found in the literature. Once more, it should be noted that estimates of S are a rough approximation of the real safety margins and significant deviations between predicted and observed values for the a^*-d^* relationship may therefore be expected.

2.2.2.3 Units of the biomechanical model

For the model to be dimensionally consistent, an approach similar to White and Gould (1965) was followed. Ordinarily since D in Eq. (2.4c) is a length, $D^{2.689-d^*}$ can not be. The dimensional equivalent of Eq. (2.4c) reads as [kg] = [kg] [kg] [cm] $[cm]^{-2}$ $[cm]^{2.689-d^*}$ or 1 = [kg] $[cm]^{0.689-d^*}$ since S is a dimensionless variable. To ensure compatibility of the model, White and Gould (1965) introduced a conversion factor q_o with a value equal to unity; for the aforementioned equation q_o = 1 $[kg]^{-1}$ $[cm]^{d^*-0.689}$ and the units in Eq. (2.4c) are therefore balanced.

2.2.2.4 Validation of the biomechanical model

To validate the biomechanical model, 123 allometric regressions that relate M_S to D, reported by Ter-Mikaelian and Korzukhin (1997), were used. These equations were based on tree scale-data and had been developed for several broadleaf and conifer species growing in USA. The biomechanical model ($a^* = z^{d^*}(K/S)D^{2+Bcr-d^*}$), was applied to each d^* value reported in the Ter-Mikaelian and Korzukhin (1997) database, and for three different diameters (smallest, average, largest). In Figure 2.3, the modelled and the real a^* values are plotted against the corresponding d^* values. The diameter is expressed in centimetres, and the fitted empirical curve on the linear scale reads as $a^* = 1.5451d^{*\,-3.4484}$, with $R^2 = 0.59$. It is clear from this Figure that when the smallest diameter is used in the model (for each reported equation), a large deviation between the predicted and the real a^* values occurs. On the contrary, large and average-size trees, give very good qualitative agreement between the modelled and real values. The modelled allometric constants tend to follow a similar overall pattern as the observed ones.

To examine further the relationship between theoretical and real a^* values, a simple linear regression analysis was done. The results of the regression indicated that the modelled and the observed values were not correlated when I used the smallest value of diameter in the biomechanical model for every reported regression (Figure 2.4A). Better predictions were obtained when the diameter values from the average and large trees were used (77 and 74 %, respectively). However, when an outlier pair of the allometric coefficients was removed ($a^* = 0.5788$, $d^* = 2.3151$), then the model explained more than 80% of the variability in the a^* values when the average and the largest values of D were used (Figure 2.4 B, C). The confidence interval at 95% level for the regression constant presented in Figure 2.4B is from -0.044 to -0.015, while for the slope estimate the 95% level interval is from 1.039 to 1.29. The computed 95 % confidence interval for the constant estimate in Figure 2.4C is from –0.094 to –0.048 and for the slope the 95% lower limit is 1.5137 while the upper limit is

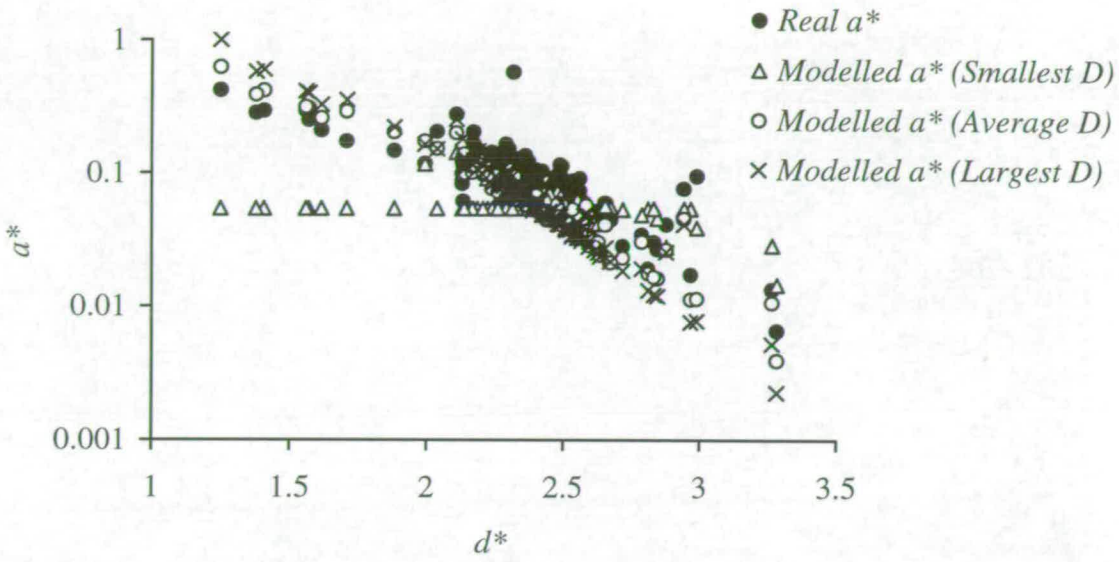

Figure 2.3: Modelled (from the biomechanical model) and real a^* against d^*. Data reported by Ter-Mikalean and Korzukhin (1997). The diameter is expressed in centimetres. The number of a^*-d^* pairs is 123.

1.9095. The model would produce precise and unbiased estimates for the observed allometric coefficients a^*, if the slope and the constant in Figure 2.4B and Figure 2.4C were not statistically different from one and zero, respectively. In general, the model slightly overestimated the measured a^* values (as indicated from the 95 % confidence intervals of the slope estimates) when the diameters from the average and large trees were used. The biomechanical model was also run with D expressed in different measurement units (namely, millimetre, decimetre and metre). In Table 2.3, different statistics obtained from the regression between modelled and real a^* values are presented.

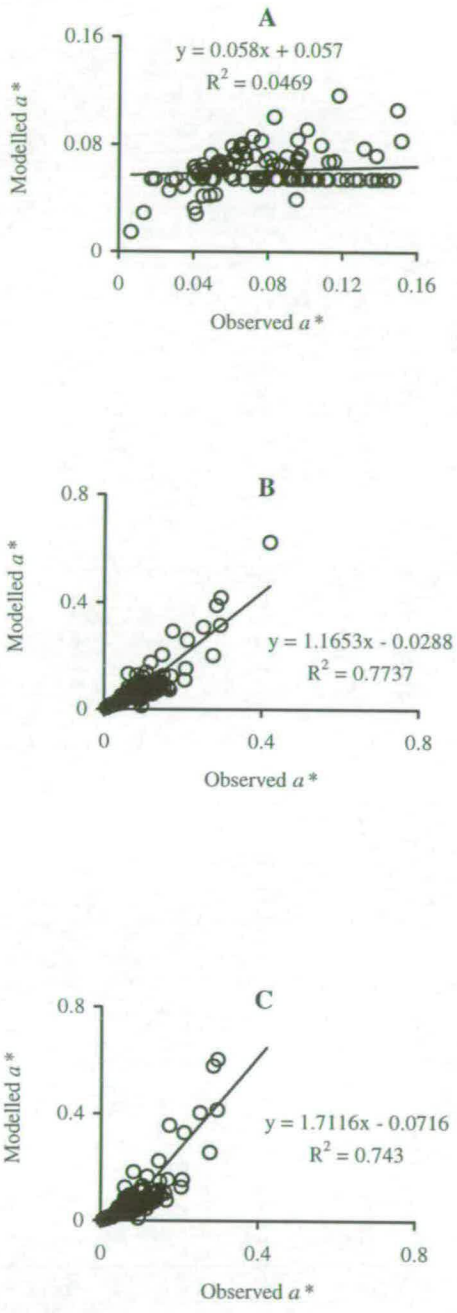

Figure 2.4: Modelled vs. real a^* values, when the smallest (**A**), the average (**B**) or the largest (**C**) diameter are used in the biomechanical model. The diameter is expressed in centimetres. The data were reported by Ter-Mikalean and Korzukhin (1997).

Table 2.3: Statistics computed for the regression between the modelled (dependent variable) and observed (independent variable) a^* values. The model was run for three different measurement units for D, namely millimetres, decimetres and metres. The coefficient of determination is denoted as R^2 and the confidence interval (at the 95% level) as CI.

Units	Diameter	Intercept	95% CI (Intercept)		Slope	95% CI (Slope)		R^2
mm	Smallest	23×10^{-5}	19×10^{-5}	25×10^{-5}	0.14	0.13	0.15	0.86
	Average	-4×10^{-4}	-5×10^{-4}	-2×10^{-4}	1.72	1.66	1.77	0.97
	Largest	-7×10^{-4}	-9×10^{-4}	-4×10^{-4}	2.17	2.09	2.24	0.96
dm	Smallest	13.00	9.71	16.29	0.18	0.04	0.31	0.05
	Average	13.79	12.11	15.45	0.10	0.03	0.17	0.08
	Largest	13.32	11.79	14.84	0.07	0.01	0.13	0.05
m	Smallest	-1590.2	-3514.6	334.07	1.29	1.09	1.49	0.82
	Average	502.89	-88.81	1094.61	0.65	0.59	0.71	0.82
	Largest	1382.9	1037.38	1728.4	0.4	0.37	0.44	0.83

Again, three different diameters (smallest, average, largest) were used to predict a^* for each d^* value. It is clear from Table 2.3 that with D in decimetres the model does not accurately predict the reported variability in a^* values. Better estimates are reported for the average and largest diameter with D in millimetres scale, since the biomechanical model explains 96% of the variability observed in the real values. However, the slope of the regression in the observed versus modelled values plot, is statistically different from unity and about twice this value, indicating that the model overestimates the empirical a^* estimates (see Table 2.3).

When the smallest diameter is used, then an underestimation (by a factor of about 0.14) is reported. Very good predictions are obtained when the diameter is measured in metres and the smallest trees are used. In this case, the model explains 82% of the variability in a^* values, and the 95% confidence interval for the slope is from 1.09 to 1.49, implying that only slight overestimation of the real values occurred. The intercept is not statistically different (at the 95% level) from zero.

So far, the model has been run with the safety factor values (S) that are reported in Table 2.2. Considering the interspecific 'nature' of the collected a^*-d^* empirical values, it is worthwhile to validate the biomechanical model against the 'average' tree. In other words, the average S value computed from Table 2.2, was applied to the model, using the average diameter value for each compiled equation and the average wood density and form factor (as explained in Section 2.2.2.2). The summary statistics of the ordinary least squares regression of observed versus predicted a^* values are reported in Table 2.4.

Table 2.4: Statistics computed for the regression between the modelled (dependent variable) and observed (independent variable) a^* values. The average values for the parameters of the model (S, f, ρ, D) were used in this analysis.

Units	Diameter	Intercept	95% CI (Intercept)		Slope	95% CI (Slope)		R^2
mm	Average	-10^{-4}	-2×10^{-4}	1.37×10^{-6}	1.01	0.94	1.04	0.97
cm	Average	-0.0039	-0.014	0.006	0.88	0.79	0.98	0.80
dm	Average	11.74	9.78	13.7	0.19	0.10	0.28	0.12
m	Average	1965.4	1520.1	2392.7	0.38	0.34	0.43	0.74

The model gave the best predictions with D expressed in millimetres scale, as indicated by the coefficient of determination (97%) and the intercept and slope values (0.0001 and 1.01, respectively). Very good estimates were also obtained when diameter is expressed in centimetres, since the statistics of the regression between observed and predicted a^*, show only a slight underestimation (slope = 0.88) of the real values (R^2 = 80%, intercept = -0.0039). With D expressed in metre, the model tended to underestimate the observed values by a factor of *ca* 2000. If the diameter is expressed in decimetres the biomechanical model failed to predict accurately the real a^* values (R^2 = 14%), but, as depicted in Figure 2.5, predicted values follow, in general, the observed trend in a^*-d^* relationship. There is a fairly good qualitative agreement between the predicted and the real a^*-d^* trajectories. Both trends tend to follow a similar overall pattern, with the exception of a simple outlier value. The mathematical artefact, inherent in the equation that describes the empirical a^*-d^*

relationship, greatly affects the correlation between the allometric coefficients. For example, the coefficient of determination in Figure 2.5 (for the real a^*-d^* pairs) is 12%, but despite this artefact influence, the modelled a^* values were within the observed range and no extreme values are therefore depicted.

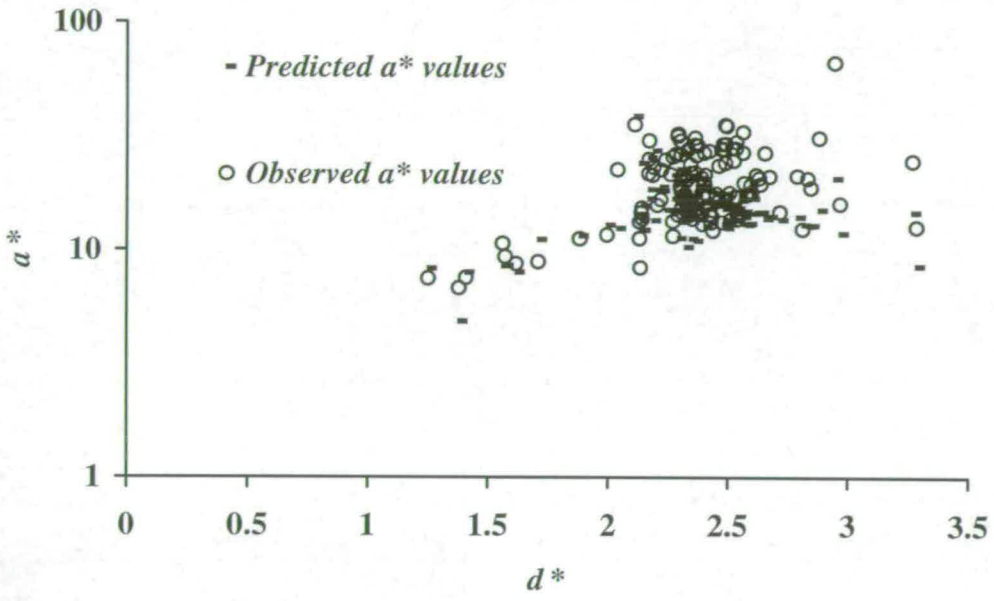

Figure 2.5: Modelled and real a^* values in relation to d^*. The average values for the parameters of the model were used and the diameter was expressed in decimetres. The number of a^* - d^* pairs is 123.

Assuming that the same biomechanical principles are valid both for the stem and total aboveground tree biomass, I applied the biomechanical model (Eq. 2.4b) to the empirical values of the allometric coefficients a and b that had been reported for the M-D regression (*i.e.*, $M = aD^b$) developed throughout the globe (Table A1 in Appendix). In 54 equations the D range was not reported and thus only 225 pairs of a-b values were used in this analysis. Three different diameter classes (smallest, average, largest) for each compiled equation were used, and the model was run with four different units namely, millimetre, centimetre, decimetre and metre. The observed a values were regressed against the predicted and the ordinary least squares method was employed in order to examine the performance of the model. In Table

2.5 the statistical properties of the regression between observed and corresponding predicted *a* values are reported. Unbiased and accurate predictions (in relation to empirical observations) are obtained if the slope and the intercept is statistically different from one and zero, respectively.

Table 2.5: Statistics computed for the regression between the modelled (dependent variable) and observed (independent variable) *a* values. The model was run for three different measurement units for *D*, namely millimetres, decimetres and metres. The coefficient of determination is denoted as R^2 and the confidence interval (at the 95% level) as CI. The number of *a-b* pairs is 225.

Units	Diameter	Intercept	95% CI (Intercept)		Slope	95% CI (Slope)		R^2
mm	Smallest	2×10^{-4}	2×10^{-4}	3×10^{-4}	0.13	0.11	0.15	0.55
	Average	4.1×10^{-4}	-5×10^{-4}	-2×10^{-4}	1.09	1.04	1.13	0.92
	Largest	-5×10^{-4}	-6×10^{-4}	-4×10^{-4}	1.27	1.22	1.33	0.92
cm	Smallest	0.045	0.04	0.05	0.14	0.11	0.17	0.32
	Average	-0.0095	-0.01	0.0007	0.62	0.56	0.68	0.71
	Largest	-0.035	-0.04	-0.02	0.88	0.80	0.96	0.70
dm	Smallest	13.37	10.65	16.08	0.10	0.01	0.19	0.02
	Average	13.80	12.07	15.50	0.09	-0.02	0.09	0.008
	Largest	11.84	9.80	13.88	0.11	0.04	0.18	0.05
m	Smallest	-569.48	-1222.9	83.92	0.72	0.64	0.80	0.64
	Average	1385.2	947.6	1822.8	0.31	0.25	0.36	0.42
	Largest	1882.4	1045.2	2119.3	0.22	0.20	0.25	0.77

The best predictions were obtained for the average diameter when it was expressed in millimetres. The predicted *a* values explain more than 92% of the variability in the empirical allometric constants and no bias or overestimation results (the slope is very close to 1 and the intercept is equal to –0.0004). If the diameter is expressed in other units, the performance of the model ranges from fairly good (centimetre and metre scales) to total inconsistency with the real values (decimetre scale).

2.2.3 Models based on fractal geometry

Traditionally, stem form has been approximated by a number of geometric features belonging to the family described as solids of revolution (quadratic and cubic paraboloid, neiloid, cone, *etc.*), and tools provided by the Euclidian geometry are considered to be appropriate to describe the interrelations between its dimensions. On the other hand, classical geometry fails to illustrate the inner details of tree crowns and when we model tree shape as a whole – by taking into account the photosynthetic units, *viz.* stem plus crown. For example a cone-like or ellipsoid-like shape is usually assumed in crown modelling studies despite the fact that crown volume encompasses mostly empty space. According to fractal geometry (Mandelbrot, 1983), a tree crown can be depicted as a hybrid object between surface and volume and several analytical procedures for the determination of its dimension are described by Zeide and his co-workers (Zeide and Gresham, 1991; Zeide and Pfeifer, 1991; Zeide, 1993; Zeide, 1998; see also Chapter 1). In the following Section, assumptions and predictions made from a model, which was presented by West *et al.* (1999) - the WBE model - and based on the fractal properties of branching patterns, is briefly described. Finally, concepts and ideas related to the fractal dimensions of tree structure are employed in order to develop a straightforward equation, which is termed here the 'reductionist' model.

2.2.3.1 The WBE *model*

In this Section a brief description of the WBE model, which was developed by West *et al.* (1999), is presented. This model was built in order to predict the allometric relationships of many structural and functional attributes, both among branches within a plant and between plants differing in size. The model is based on the transport processes of essential materials through branching vascular networks, and is an extension of a zeroth-order general model developed to simulate resource distribution systems found in organisms (West *et al.*, 1997). A hierarchical branching network running from the trunk to the petioles is the basic framework of the plant model (Figure 2.6). The model assumes that:

i) the xylem network system is composed of microtubular vascular elements aligned in parallel and running from rootlet to leaf;
ii) all tubes are considered to have equal length, and their diameters are constant, within a branch segment but allowed to vary between segments, resulting in tapering of tubes from trunk to petiole and
iii) the proportion of conducting to nonconducting tissue is allowed to vary so as to resolve possible conflicts between biomechanical and hydraulic constraints.

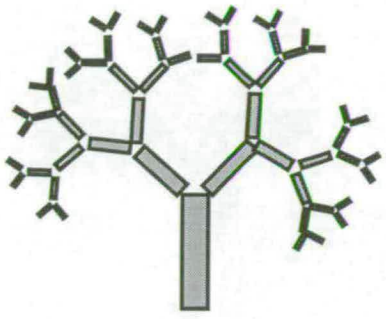

Figure 2.6: Graphical representation of the 'plant model' (modified from Enquist *et al.*, 2000).

The plant model predicts that the architecture of the branch system is a self-similar fractal object and the transport network is built in such a way so as to supply resources to all parts of the body. As a consequence, it is implied that at the higher levels of the volume filling branching structure (*i.e.*, petioles), the transport modulus occupies a three-dimensional space, and in effect, the periphery of the plant crown is exclusively occupied by bilateral shoots. In addition, it is predicted that the terminal elements of the fractal-like vascular system do not vary as body size changes, and finally the energy required to distribute materials is minimised. The authors show that as a result of these predictions, plants exhibit a common set of allometric relationships, irrespective of other factors (age, genetic variability, site quality, *etc*). For example, the model predicts that plant height scales as the 0.25-power of plant biomass, while plant diameter scales as the 3/8 power of plant mass, and these values are considered to hold valid both in the interspecific and intraspecific context. Some

comments on the assumptions and predictions made by the plant model are presented in the 'Discussion' Section of this Chapter.

2.2.3.2 Validation of the WBE *model*

According to the WBE model, total aboveground tree biomass scales as the 2.67-power of D, irrespective of genetic or environmental influences. The average value for the scaling exponent, calculated from the compiled regressions in the meta-database (Table A1) is instead 2.3679. The standard error of 0.0163, indicates that there is a significant difference ($P< 0.001$; t-test) between the WBE modelled value and the empirical value of the parameter (Table 2.6). Moreover, as it is shown in Figure 2.7, about 77% of the collected b values fall in the range 2-2.6, while *ca* 16% fall in the range from 2.72 to 2.96 groups. Six percent of the data had even lower values of b (*i.e.*, from 1.16 to 1.99). If we consider that the collected equations is a representative sample of the population of regressions, then we may conclude that the WBE model failed to describe the empirical data. The same analysis was carried out using the reduced major axis (RMA) values of b for the compiled equations, and results indicated (mean = 2.3883, st. dev. = 0.32) that there is still a significant difference (at 5% level) between the empirical and theoretical value ($P< 0.001$; t-test). This is hardly surprising, since the RMA values were calculated as the ratio of b over r (b/r), where r is the coefficient of correlation, which in all cases was above 0.95.

A distribution analysis for the allometric constant (a) was not made since its value depends on the units of measurement of the independent variable D, as explained in Section 2.2.2.1 (see also Figure 2.2). This dependency also holds true when we study the regression of stem mass on D.

Table 2.6: Statistics for the allometric exponent (b), computed from the 279 compiled equations.

Statistic	Value
Mean	2.3679
Standard error of mean	0.0163
Standard deviation	0.27
Variance	4.71
Skewness	-1.016
Standard error of skewness	0.146
Kurtosis	2.774
Standard error of kurtosis	0.291

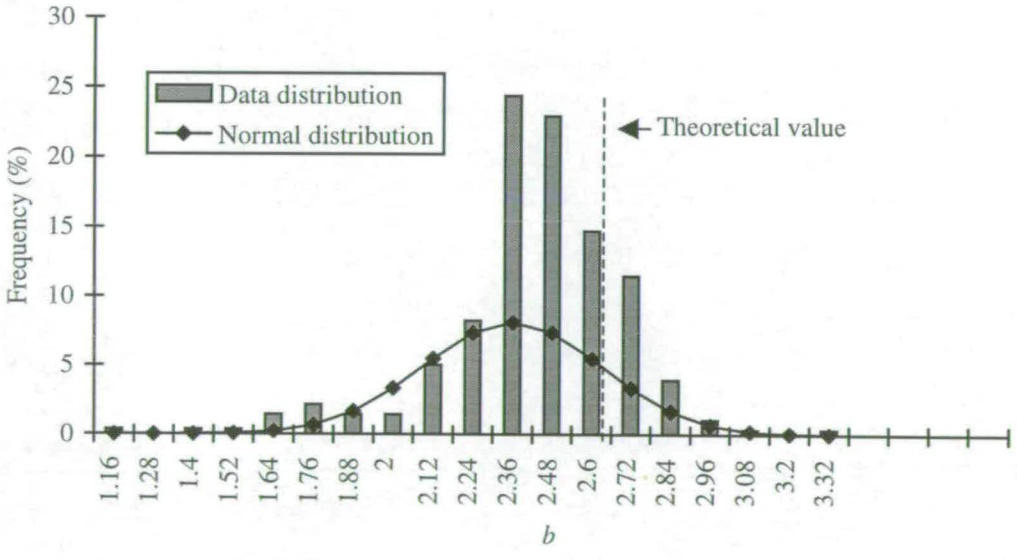

Figure 2.7: The relative frequency distribution of b values reported in the compiled equations is superimposed on the normal curve.

2.2.3.3 Development of the 'reductionist' model

In this Section, insights provided by fractal geometry (Mandelbrot, 1983) and from the biomechanical principles of tree structure are presented and a 'reductionist' model describing tree size-shape relationships is developed. According to simple dimensional analysis, the volume of a tree is, $V_T \propto D^2H$. Moreover, dimensional analysis assumes that the cross-section of the stem at breast height is an idealised geometric object (circle, ellipse, *etc.*), and its area A is related to the circumference P by $A \propto P^2$. In effect, D (which is also a linear dimension of the cross-section) is also related to A by $A \propto D^2$.

However, this is not completely true for real trees since the stem cross-section at any height has a non-standard shape that can not be approximated by ideal objects. Mandelbrot (1983) suggested that the description of natural objects falls beyond the principles provided by Euclidean geometry and introduced the neologism (and related concepts) of fractal geometry to facilitate the understanding of the form and shape of these objects.

Based on fractal geometry analysis, several techniques have been developed to quantify the dimensions of trees while the usefulness of fractal geometry in ecological studies has been demonstrated several times (*e.g.* Zeide and Gresham, 1991; Zeide and Pfeifer, 1991; Zeide, 1993; Osawa, 1995; Berezovskava *et al.*, 1997; Zeide, 1998). For the sake of simplicity - since no information is yet available - the dimension of the stem volume may be approximated by the third power of its linear dimension. On the other hand, it is generally acknowledged (Mandelbrot, 1983; Zeide and Gresham, 1991; Zeide and Pfeifer, 1991; Zeide, 1993; Osawa, 1995; Zeide, 1998) that a positive number between 2 and 3 is a better estimation of the crown dimension of trees and according to fractal analysis the overall shape of a tree (stem and crown) may possess a similar fractal dimension. In mathematical terms

$$V_T \propto D^d H^h \qquad \text{Eq. (2.5)}$$

where d and h are positive numbers with $2 < d+h < 3$.
Across a range of species, ages and site conditions, we may also assume that:

$$d + h = 2.5 \qquad \text{Eq. (2.6)}$$

(*cf.* Zeide and Gresham, 1991).

Theoretically, tree shapes and particularly tree crowns can be described as hybrid objects of surface and volume, since they are neither three-dimensional solids, nor two-dimensional photosynthetic surfaces (Zeide, 1998) - indentations and gaps are the main characteristics of their structure.

Following biomechanical principles of the tree structure, the scaling of H with respect to D has been examined principally in terms of stress and elastic similarity models (McMahon and Kronauer, 1976). Niklas (1994) reported that H scales as the 0.535 power of D for a wide range of plant sizes. If $H \propto D^{b^*}$ with $0 < b^* < 1$, then Eq. (2.5) becomes

$$V_T \propto D^d D^{hb^*} = D^{d+hb^*} \qquad \text{Eq. (2.7)}$$

Furthermore, if tree biomass is assumed to be proportional to V (tree density as the proportionality constant) then $M \propto D^{d+hb^*}$ and in conjunction with the equation that relates M to D (*i.e.*, $M = aD^b$)

$$b = d+hb^* \qquad \text{Eq. (2.8).}$$

Two predictions arise from this analysis:
i) the scaling coefficient between M and D depends on the scaling coefficient between H and D (as proposed by Ketterings *et al.* (2001) without testing) and

ii) the sum of the intercept d and the slope h of the b-b^* relationship should yield 2.5, which is the average fractal dimension of trees (as proposed by Zeide and Gresham, 1991).

In practical terms, the allometric exponent in H-D relationship, namely b^*, can be used in order to estimate the allometric parameters in M-D allometry and subsequently to estimate the M value for a given D. The procedure is straightforward and its applicability is presented in Section 2.3.2.

2.2.3.4 Calibrating the 'reductionist' model

To calibrate the reductionist model (Eq. 2.8), values for the allometric parameter b and the corresponding parameter b^* were used for each study presented in Table 2.7. The range for the compiled b^* values is from 0.2596 to 1.07 while the b parameter falls in between 2.0392 and 2.7017. As is depicted in Figure 2.7, about 88% of the collected 279 b values (Table A1), fall into this range. Thus, the compiled b-b^* pairs may accurately represent the population of the allometric exponents in biomass-diameter and height-diameter relationships. The regression line between b and b^* is illustrated in Figure 2.8 and the statistical parameters are reported in Table 2.8. The ordinary least squares method was used to fit the curve in the reported values.

A strong linear relationship (R^2 = 66%) is obtained between the b and b^* values with a positive trend. More interesting, the sum of the two coefficients in this linear relationship equals 2.6062, which is a value very close to the theoretical one (2.5), that was derived using fractal analysis of tree dimensions. Moreover, it is statistically substantiated that the scaling exponent between M and D depends on the scaling exponent between H and D - as proposed by Ketterings *et al.* (2001) but without thorough testing.

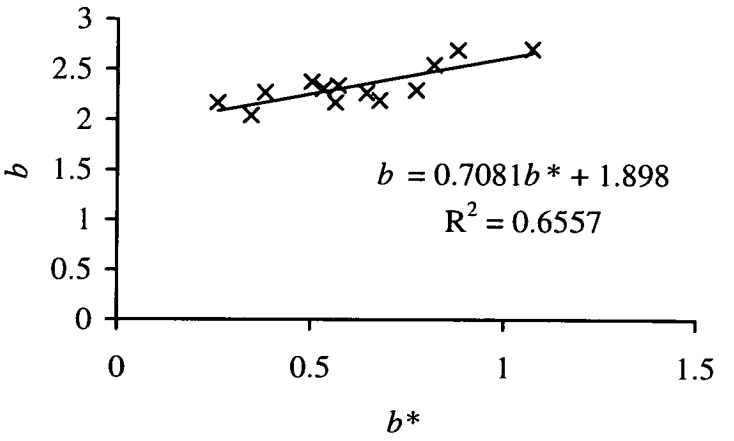

Figure 2.8: The regression line of b versus b^* from data reported in 13 empirical studies (Table 2.7). The ordinary least squares method was used to fit the curve.

Table 2.7: Thirteen studies on tree size-shape relation were reviewed for the calibration of the equation between the scaling exponents b and b^* found in *M-D* and *H-D* relationships, respectively.

No	Author	*n*	Species	*b**	*b*
[1]	Cantiani (1974)	21	*A. alba*	0.3814	2.2716
[2]	Makela and Vanninen (1998)	48	*P. sylvestris*	0.8802	2.6931
[3]	Vanninen *et al.* (1996)	48	*P. sylvestris*	1.0746	2.7017
[4]	Parresol (1999)	39	*Q. phellos*	0.2596	2.1702
[5]	Taras (1980)	6	*P. clausa*	0.5024	2.3789
[6]	Menguzzato and Tabacchi (1988)	17	*P. radiata*	0.7725	2.2936
[7]	Menguzzato and Tabacchi (1988)	68	*Eucalyptus*	0.6443	2.2644
[8]	Baldini *et al.* (1989)	8	*P. pinaster*	0.3459	2.0392
[9]	Whittaker and Woodwell (1968)	15	*P. rigida*	0.5699	2.3373
[10]	Whittaker and Woodwell (1968)	15	*Q. coccinea*	0.6783	2.19
[11]	Whittaker and Woodwell (1968)	15	*Q. alba*	0.5629	2.1666
[12]	Tahvanainen (1996)	154	*Salix spp.*	0.8188	2.54
[13]	This thesis	16	*F. moesiaca*	0.5317	2.3087

Table 2.8: Statistics computed for the regression between the b^* (independent variable) and b (dependent variable) values as reported in Table 2.7. The coefficient of determination is denoted as R^2 and the confidence interval (at the 95% level) as CI.

Intercept	95% CI (Intercept)		Slope	95% CI (Slope)		R^2
1.898	1.6805	2.1154	0.7081	0.3763	1.04	0.66

2.2.3.5 Validating the 'reductionist' model

The pooled data (223 trees in total) from the ten compiled studies presented in Table 2.9, were used in order to develop a simple allometric model for the *H-D* relationship.

Table 2.9: Ten allometric studies that report raw data at tree-level. The parameters a and b denote the allometric coefficient and allometric exponent in *M-D* relationship, respectively; b^* denotes the allometric exponent in *H-D* relationship; R^2 and R^2* are the coefficient of determination in *M-D* and *H-D*, respectively; n is the number of harvested trees.

No	Species	Region	a	b	b^*	D (cm)	R^2	R^2*	n
[1]	Spruce	USA	0.1062	2.3574	0.8486	2.9-23	0.9835	0.9071	31
[2]	Aspen	USA	0.036	2.785	0.5938	5.8-23.7	0.9915	0.9183	8
[3]	Aspen	USA	0.1061	2.4151	0.6847	0.9-35.4	0.9942	0.9784	32
[4]	Scots pine	UK	0.196	2.2055	0.4324	6.3-25.6	0.9809	0.8025	22
[5]	Scots pine	SPAIN	0.2375	2.0291	0.6469	2.5-36.5	0.9914	0.8986	7
[6]	Beech	SPAIN	0.1315	2.432	0.5602	4-34.5	0.9983	0.886	7
[7]	Birch	USA	0.0809	2.3595	0.4926	7.1-23.1	0.9704	0.7604	15
[8]	Douglas fir	ITALY	0.1413	2.2996	0.3733	8.7-26.8	0.9493	0.9994	69
[9]	Nor. spruce	CZECH REB.	0.2161	2.1864	0.5256	13-41.5	0.9858	0.903	11
[10]	Trop. species	INDONESIA	0.0639	2.5866	0.6094	7.6-48.1	0.9522	0.6852	29

Number of studies correspond to: [1] Woods *et al.* (1991); [2] Gower (pers. comm.); [3] Woods *et al.* (1991); [4] Lim (1979); [5] Santa Regina and Tarazona (2001a); [6] Santa Regina and Tarazona (2001b); [7] Jokela *et al.* (1981); [8] Menguzzato and Tabacchi (1986); [9] Cerny *et al.* (2000); [10] Ketterings *et al.* (2000).

The mathematical equation takes the form $H = 2.3927D^{0.6504}$ with $R^2 = 85\%$. The diameter range is 0.9-48.1 cm and the height range from 2.2 to 32.4 m. The allometric exponent of the aforementioned relation (0.6504) was used in the empirical equation that describes the relationship between b and b^* ($b = 0.7081b^* + 1.898$, Figure 2.8) in order to derive a 'reductionist' slope for the *M-D* relationship. The predicted b value was subsequently applied to the biomechanical model (Eq.

2.4b, using average values for S, f, ρ, D) to estimate the a value in the M-D relation for the pooled dataset (223 trees). The real and the predicted a-b pairs are reported in Table 2.10.

Table 2.10: Predicted and observed values of the allometric parameters in the M-D relationship. For the observed values the OLS regression was applied to 223 trees (see Table 2.9). Predicted values were derived from the 'reductionist' and the biomechanical model.

	a	b
Observed	0.1054	2.3972
Predicted	0.0973	2.3586

For each diameter, the predicted allometric coefficients (a and b), derived from the reductionist and biomechanical model, were applied to Eq. 2.1. Thus, for each tree the real value of the total aboveground biomass was regressed against the corresponding modelled one. In Figure 2.9, the model M values were derived from Eq. 2.1 by entering the predicted a and b values, which are reported in Table 2.10.

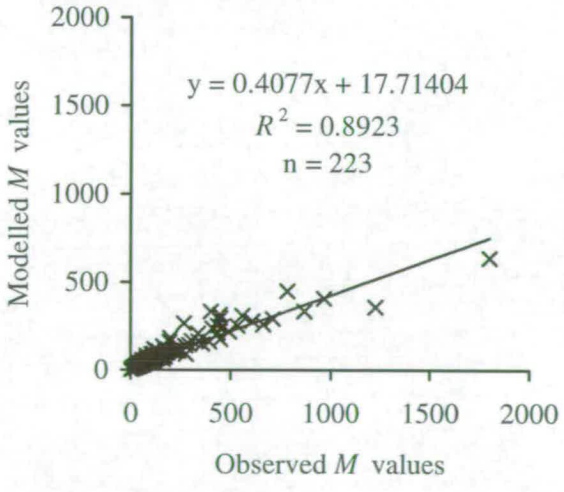

Figure 2.9: Regression of modelled on real M values. Modelled M values are derived through Eq. 2.1 with the predicted allometric parameters reported in Table 2.10.

The slope of the regression line in Figure 2.9 indicates that the modelled values underestimate the real total biomass of the 223 trees. On average, the modelled values deviate about 40% in relation to the real total aboveground biomass estimates. However, if the largest diameter of the 223 collected trees (namely 48.1 cm), is used in the biomechanical model (instead of the average D), the predicted estimates will deviate, on average, by 22% from the real M values. For comparison, the mean percentage difference between regressed and real M values is 18%. Thus, bearing in mind that this analysis was made on a diverse compendium of trees, which have different structural and functional characteristics, (broadleaves versus conifers, and temperate versus tropical species), is supported that the model can capture most of the variability occurring in the tree total aboveground biomass, if accurately parameterised. So far, the b-b^* relationship was used for the interspecific comparison between real and modelled M values. This approach was necessary so as to understand better the size-biomass interrelation of terrestrial trees. Its usefulness in estimating the total aboveground biomass at the stand-scale is explained in more detail in Section (2.3.2).

2.3 THE USEFULNESS OF SIZE-SHAPE MODELS IN BIOMASS STUDIES

2.3.1 WBE model versus empirical approaches in predicting M

Theoretical analysis of the variables describing tree structure was employed to derive aboveground biomass predictions. The WBE model described in Section 2.2.3.1 predicts that M scales as the 2.67 power of D, but no value is given for the scaling coefficient, a. However, Chambers *et al.* (2000) reported that a is *ca* 0.1002 when D is expressed in cm - irrespective of species and site - and this value was used to obtain theoretical predictions of M for tree diameter. This pair of a-b values will be referred to as the WBE prediction (or approach).

On the other hand, the averages of a and b parameters calculated from the 279 empirical values presented in Table A1 were used to estimate M from D for each of the ten studies. This pair of a-b values will be referred to as the empirical prediction

(or approach). Predictions made by the WBE and empirical approaches were validated against the tree-scale data of the ten datasets presented in see Table 2.9. The MPD criterion (symbol Π) was used to illustrate the degree of deviation between predictions (made by the empirical and the theoretical approach) and the raw data.

$$\Pi = |M - \hat{M}|/M$$

where M and $\hat{M}$ denote the real and the predicted biomass for a particular diameter, respectively. Results for the two models are summarised in Table 2.11. MPD values for the regressions that were based on several trees, for each study, are also reported.

Table 2.11: Validation of the WBE and empirical model. The mean percentage difference (MPD,%) for the OLS regression (Reg.), the theoretical (WBE) and the empirical (*i.e.*, $M = 0.1469D^{2.3679}$) equations (Emp.) are presented in the last three columns respectively. For more information on the biomass studies see Table 2.9.

Study	Source	Species	Reg.	WBE	Emp.
[1]	Woods *et al.* (1991)	Spruce	13%	104%	45%
[2]	Gower (person. comm.)	Aspen	8%	107%	41%
[3]	Woods *et al.* (1991)	Aspen	15%	83%	28%
[4]	Lim (1979)	Scots pine	9%	81%	18%
[5]	Santa Regina and Tarazona (2001a)	Scots pine	13%	209%	77%
[6]	Santa Regina and Tarazona (2001b)	Beech	5%	48%	8%
[7]	Jokela *et al.* (1981)	Paper birch	10%	187%	87%
[8]	Menguzzato and Tabacchi (1986)	Douglas-fir	9%	98%	26%
[9]	Cerny *et al.* (2000)	Nor. spruce	7%	120%	21%
[10]	Ketterings *et al.* (2001)	Tropical	28%	111%	37%
[11]	Pooled data	-	18%	106%	35%

Mean percentage difference between WBE and observed values for the compiled studies fell in the range 48-209%, while deviations for the empirical model (*i.e.*, $M = 0.1469D^{2.3679}$) were in the range between 8 and 87% (Table 2.11). Pastor *et al.*

(1983/1984), reported that the maximum value of MPD for regressions based on raw data is *ca* 35%, and consequently the WBE model failed to predict accurately *M* values for all datasets. The empirical model performed within moderate levels of accuracy (except in study 5 and study 7, Table 2.11) as compared to the MPD values of the regressed equations. In 5 out of 10 studies the MPD was smaller that 35% and slightly above the acceptable limit in the 10^{th} dataset (37%). The best predictions were obtained for a beech stand (study 6) and the larger MPD was calculated for paper birch (Study 7 with $I\!I = 87\%$). Whether differences in MPD values among studies are due to anatomical or morphological characters (wood density, branchiness, age, *etc.*) or to any other subtle variable is difficult to ascertain, since not enough information was available for this kind of analysis.

2.3.2 The performance of the 'reductionist' model in predicting *M*

The correlation of the parameters *a* and *b* in regressions describing *M-D* relations provides the basic tool for the simplification of allometric analyses of forest biomass. Since pairs of *a* and *b* are restricted to a defined range of values, then inevitably *M-D* relationships can fall on only a finite number of power functions. Thus, for a particular value of *a,* only a limited range of values for *b* can be obtained. This suggests that only a limited number of *M-D* solutions exists despite the diversity of factors acting on each stand. In other words, information provided by the collected allometric equations may be useful in estimating *a* and *b* for any particular stand. Predictions for *b* for the stand under investigation can be derived through *b** (which is the allometric exponent in the *H-D* relationship) as explained in Section 2.2.3.3.. To test this method, ten studies were retrieved from the literature (Table 2.9). These studies reported original tree-level data for diameter, height and biomass values for several tree compartments. For each study the coefficient *b** was calculated from the empirical *D-H* pairs. The equation relating *b* to *b** (presented in Figure 2.8) was then employed to estimate the value of b_{red} for each *b**. Subsequently, these values were applied to the *a-b* relationship and the coefficient a_{red} was obtain for each study. To determine the differences between biomass estimation by the reductionist model and empirical total aboveground biomass values, the MPD criterion was also computed.

The first step to apply the 'reductionist' model is to parameterise the *a-b* relationship (from Table A1) and the *b-b** relationship (from Figure 2.8). The equations obtained are the following:

$$b = 1.898+0.7081b^* \qquad (R^2 = 0.6557) \qquad \text{Eq. (2.9)}$$

and

$$a = 7.0281b^{-4.7558} \qquad (R^2 = 0.6984) \qquad \text{Eq. (2.10)}$$

The b^* values which were reported in ten independent studies (Table 2.9) were applied to Eq. (2.9) to derive estimates for the b parameter; subsequently these estimates were entered in Eq. (2.10) and values for the parameter a were computed. Finally, the estimated a and b values were used to predict aboveground biomass for each diameter found in ten studies (Table 2.9) through Eq. (2.1). The summarised results for M estimation and the MPD criterion for the reductionist model, are given in Table 2.12. As it is illustrated in Table 2.12, the MPD values for the reductionist model - in 8 out of 10 studies - was below 35%, which is the maximum percentage deviation reported for regressions based on destructive sampling. In studies 5 and 7 the MPD was *ca* 45% and 41% respectively, but not far away from the aforementioned limit. It should be noted that in study 7 the R^{2*} (which stands for the coefficient of determination in *H-D* relation, see Table 2.9) has a value of 0.76. In other words the b^* used for this study may not accurately represent the *H-D* relation of the sampled trees and in effect may strongly influence the miscalculation of a and b parameters.

Table 2.12: The mean percentage difference for the regression (MPDREG) and reductionist model (MPDRED) are presented in the last two columns, respectively. For each study the allometric exponent b_{red} was computed with Eq. (2.9) and the allometric coefficient a_{red} with Eq. (2.10). Study numbers correspond to Table 2.9; a_{reg} and b_{reg} were calculated with the OLS method.

Study	b^*	a_{reg}	a_{red}	b_{reg}	b_{red}	MPDREG	MPDRED
[1]	0.8486	0.1062	0.0887	2.3574	2.5076	13%	25%
[2]	0.5938	0.036	0.1232	2.785	2.3401	8%	20%
[3]	0.6847	0.1061	0.1093	2.4151	2.3999	15%	15%
[4]	0.4324	0.196	0.1536	2.2055	2.2341	9%	15%
[5]	0.6469	0.2375	0.1148	2.0291	2.375	13%	45%
[6]	0.5602	0.1315	0.1287	2.432	2.3181	5%	27%
[7]	0.4926	0.0809	0.1413	2.3595	2.2736	10%	41%
[8]	0.3733	0.1413	0.167	2.2996	2.1953	9%	13%
[9]	0.5256	0.2161	0.1351	2.1864	2.2953	7%	11%
[10]	0.6094	0.0639	0.1207	2.5866	2.3504	28%	29%

On the other hand, the R^2* of the 10th dataset has the smallest value (0.68) of all the compiled equations but quite accurate predictions of the M variable were obtained (MPD = 29% for the reductionist and 28% for the regression). The most accurate predictions for aboveground tree biomass was made in the 9th dataset (MPD = 11%) even though b_{reg} and b_{red} as well as a_{reg} and a_{red} are totally different. However, the absolute difference between the MPD of the two models is only 4%. This is also the case for the 10th study where the a_{red} is about twice the a_{reg} and b_{reg} much larger than b_{red} but the two models gave the same level of accuracy as implied by the MPD values. Finally, in the 3rd dataset, the MPD for the reductionist and regression method is exactly the same (15%) which is to be expected since $b_{red} \approx b_{reg}$ and $a_{red} \approx a_{reg}$. A preliminary analysis failed to identify any relation between magnitude of MPD and other specific characteristics for each study (family of species, number of sampled trees, D range, *etc.*).

2.4 PHYLOGENETIC ANALYSIS OF SIZE-BIOMASS ALLOMETRY

I now turn to analysis of the allometric equations that describe the relationship between diameter at breast height (D) and total tree biomass (M), within a phylogenetic context. Scaling relationships may be drawn from ontogenetic, intraspecific, and interspecific – or higher taxonomic level – comparisons. Gould (1966) emphasised that

'...the dynamic morphology of ontogeny provides a more complete and satisfactory set of taxonomic characters than does the static form of adulthood. The parameters of the ontogenetic allometry serve as excellent quantitative characters in the description of dynamic form'.

Usually, allometric equations that relate M to D are based on sampled trees that cover a large range of ages, reflecting the ontogenetic allometry of these variables. Therefore, each equation was classified according to the family of the species for which the equation was developed, so as to examine whether the scaling exponent shows 'phyletic dependency'. The compiled allometries were classified into 27 different families and the absolute frequency in each family is presented in Table 2.13; the total number of equations is 259. This analysis was totally based on the values of the allometric exponents (see Table A1) as reported in the original reference (*i.e.*, by estimation through the ordinary least squares method), and using the technique of analysis of variance.

Moreover, biomass values for the trees with the average diameter were computed from the 259 regressions and these data were analysed using nested analysis of variance for different taxonomic levels. Each species was grouped into the corresponding genus and the average biomass for each genus was nested within families; finally each family was classified either as 'conifers' or 'broadleaves'. The 'broadleaves' included 187 observations, and 72 were classified into the 'conifers' group. The nested analysis of variance permits determination of the percentage

distribution of the variance in a character among subordinate and higher taxonomic levels.

In particular, nested analysis of variance can be used to determine the taxonomic level appropriate for scaling analysis. Niklas (1994), thoroughly explains the procedures used in this method, by providing appropriate formulas and detailed examples. For the analysis of the data presented in this Section, I have followed his methodology.

Table 2.13: Distribution of compiled equations according to the 'family' criterion. *n* denotes the number of regressions.

Family	*n*	Family	*n*
Cupressaceae	4	*Aceraceae*	22
Tiliaceae	2	*Oleaceae*	4
Rosaceae	5	*Juglandaceae*	3
Moraceae	2	*Euphorbiaceae*	1
Pinaceae	68	*Combretaceae*	1
Salicaceae	19	*Melastomataceae*	1
Magnoliaceae	3	*Guttiferae*	2
Ericaceae	1	*Cornaceae*	1
Ulmaceae	1	*Meliaceae*	1
Myrtaceae	44	*Rhizophoraceae*	4
Betulaceae	25	*Caesalpinioideae*	1
Fagaceae	36	*Celastraceae*	1
Leguminosae	3	*Casurinacea*	1
Proteacea	3		

Firstly, an ANOVA was done on the allometric coefficients between the conifers and broadleaves orders. The results are reported in Table 2.14.

Table 2.14: Analysis of variance of the allometric exponent (*b*) between the order containing conifers and broadleaves. The test of significance has been set at the 95% level. [For 20 equations of the database, the regressions were built from pooled data (*i.e.*, trees belonging to different species), and thus were not used in this analysis].

	Sum of squares	*df*	Mean square	*F*	*P*
Between orders	1.233	1	1.233	19.131	< 0.001
Within orders	16.564	257	0.064		
Total	17.797	258			

As illustrated by the F statistic, the mean value of *b* for the broadleaved species is significantly different (at the 95% level) from the mean value for *b* of the conifers. In Table 2.15 the distribution statistics of the *b* values for the two groups (broadleaves and conifers) are presented.

Table 2.15: Statistical parameters of the allometric exponent (*b*) for conifers, broadleaves and pooled equations.

	Mean	*n*	St. Dev.	St. Er.	Kurtosis
Broadleaves	2.4105	187	0.2544	0.0186	1.394
Conifers	2.2565	72	0.2526	0.02977	2.789
Pooled	2.3679	259	0.2626	0.01632	1.812

The average allometric exponent *b* for the broadleaved species, amounts to 2.4105. This is statistically different (at the 95% level) from the mean value of *b* calculated from the collected equations of the conifers (2.2565). For the pooled dataset (259 equations) the average *b* value is 2.3679 with the standard error of the mean equal to 0.01632. Subsequently, each *b* value was classified according to the family of the species and the average *b* is plotted with the corresponding standard error for the 27 compiled families (Figure 2.10).

An analysis of variance indicated that there was not a significant difference (at the 95% level) among the average *b* values of the collected families. The smallest *b* value was obtained for the *Cupressaceae* family (2.1607), while the *Celastraceae*

family attained the highest *b* (2.5428). However, this family was represented by only one species and this implies a biased *b* value. It is worth noting that the mean *b* for *Betulaceae*, *Fagaceae* and *Aceraceae* is respectively 2.4002, 2.4021, and 2.4065. The number of compiled equations ranges from 22 (*Aceraceae*) to 36 (*Fagaceae*), indicating that the aforementioned *b* values are a very good approximation of the real *b* values for each family.

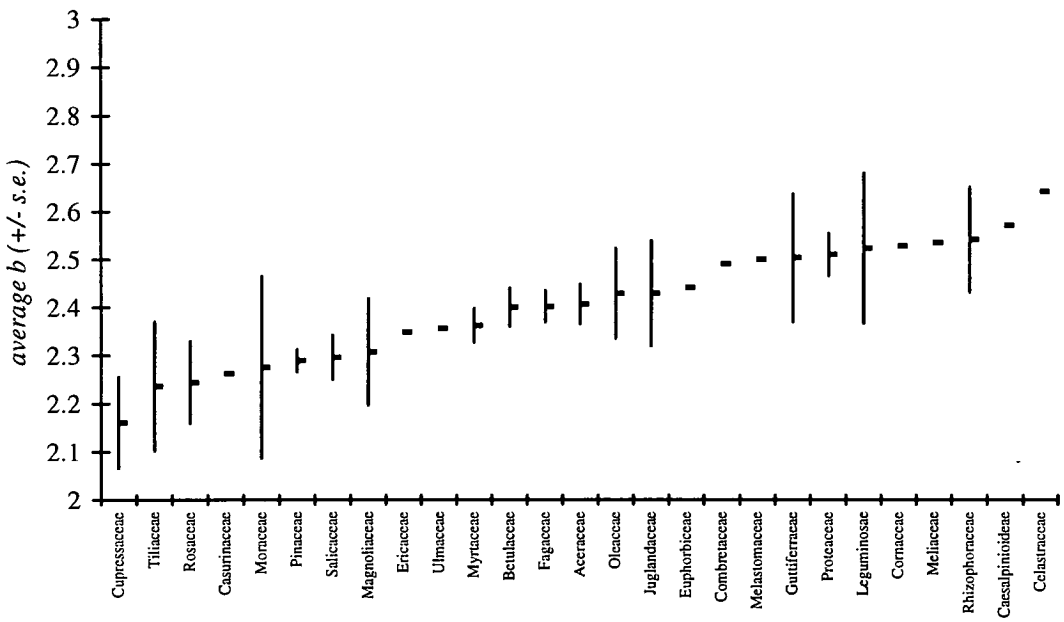

Figure 2.10: Average values of *b* calculated for 27 families. The bars indicate one standard error of the mean (+/-). No bars indicate that only one regression was found for the particular family in the literature.

However, a phyletic analysis based only on the allometric exponent (*b*) may not accurately illustrate the dependency of size-shape relationship at the taxonomic level. We should bear in mind that the allometric constant (*a*) also plays an important role in tree stature as implied by the Eq. 2.4b. To perform a taxonomic analysis on the values of allometric constant (*a*), would be a totally erroneous procedure since this parameter depends on the measurement units of tree diameter (as explained earlier,

see Figure 2.1). To circumvent this problem, the tree biomass (which is the mathematical manifestation of the interrelation between *a* and *b*) was used in the nested analysis of variance. This technique permits us to examine the distribution of variance of total tree biomass at different taxonomic levels. The results of this analysis will indicate whether and how strong the genetic variability (above genus level) influences the tree size-shape relationship. The biomass values calculated from the average diameter for each equation were used for the nested analysis of variance (Niklas, 1994). The results of the nested analysis of variance are shown in Table 2.16.

Table 2.16: Results of nested analysis variance for the biomass values of average diameter as computed from 259 allometric equations.

Source of variance	*df*	Sum of squares	Mean square
Among orders	1	27154.22	27154.22
Among families	22	1809025.6	82228.5
Within families	10	395481.1	39548.14
Total	33	2231661.2	67626.1

To calculate the percentage distribution of total aboveground tree biomass variance among the three taxonomic levels (genera, families, and orders), the mathematical procedure reported in Niklas (1994, p.357) was adopted. Thus, the percentage variance distribution among genera nested within families is approximately 50%, among families nested within orders is about 42%, and *ca* 8% is between conifers and broadleaves taxa. According to this outcome, more than 90% of the total aboveground tree biomass variability is accounted for by differences among genera within families and among families within orders.

2.5 DISCUSSION

Recently, allometric theory has provided a rapidly growing framework to examine the scaling of plant form, function and structure (Niklas, 1992; Niklas, 1994; West *et al.*, 1997). However, there is a long history of interest in allometric studies in biology. Theoretical and quantitative approaches begun almost a century ago by D'Arcy Thompson (1917) and Julian Huxley (1924), followed by Yoda *et al.* (1963), McMahon (1973 and 1975), and Causton and Venus (1981). In the endeavour to interpret scaling relations as optimal solutions to problems of mechanical design, these studies laid the foundation for the modern discipline of biomechanics. Efforts to provide a theoretical explanation for the size-shape interrelation in higher land plants, were largely or exclusively based on biomechanical principles (McMahon, 1975; McMahon and Kronauer, 1976; Bertram, 1989; Niklas 1992 and 1994). Researchers have demonstrated how physical forces of gravity and wind influence the structure of the trees (from the main trunk to the finest branches) and in turn explained how scaling relationships change within individuals (McMahon, 1975; McMahon and Kronauer, 1976; King and Loucks, 1978; Bertram, 1989; Holbrook and Putz, 1989; Niklas 1992 & 1994). However, Horn (2000) developed a totally different approach to understand the architecture and function of trees. He illustrated that simple changes in a branching 'algorithm' can give rise to trees with different morphologies that quite accurately resemble real trees.

Scientists investigating the tree size-shape relations frequently based their theories on empirical data derived either from interspecific or intraspecific specimens. In this Chapter I adopted a different approach. I tested the formulated models against information provided in the global meta-database (see Table A1) in order to illustrate whether size-biomass models may explain the empirical scaling relationships of trees growing in diverse ecological habitats.

Three different but inter-connected hypothesis have therefore been examined:

- The effect of biomechanical constraints on the tree size-biomass relationship as manifested through the biomass-diameter allometries.
- The dependency of the *M-D* equation on the *H-D* relationship which was examined through ideas provided by fractal geometry.
- The sensitivity of tree *M-D* allometry to phyletic affiliation.

In the next Sections a more detailed discussion of each hypothesis is presented.

2.5.1 On the biomechanical and WBE model

Traditionally, researchers have tried to explain the fundamental basis of scaling relations commonly found in plant form and function, by comparing observed and modelled values of the allometric exponent in Eq. 2.1. For example in Table 2.1, theoretical values for the scaling exponent in biomass-diameter and height-diameter equations have been used to examine the mechanical design of trees (McMahon, 1975; Holbrook and Putz, 1989; Niklas, 1992). Empirical data were subsequently used to speculate on the forces affecting the shape of the trees by comparing theoretical and observed values of the allometric exponent (McMahon, 1975; Bertram, 1989; Niklas, 1992; Niklas, 1994). However, the scaling constant has not received analogous attention by scientists so far, since its value depends on the units of measurement of the dependent variable in Eq. 2.1 (see Figure 2.1).

As a consequence, zoologists and paleontologists have supported the view that no biological significance can be deduced from the correlation between the allometric coefficients in Eq. 2.1 on the grounds of the mathematical artefact presented in Section 2.2.2.2 (Lumer, 1936; White and Gould, 1965; Gould, 1971). However, Lumer (1936) used as a concluding remark in his paper the following sentence:

'The biological significance of the relationship is nevertheless of importance, and the problem merits further investigation.'

White and Gould (1965), derived a similarity criterion in order to prove mathematically the biological significance of the allometric constant *a*. However, their criterion assumes that the empirical allometric exponents *b* should be equal for the scaling equations under investigation (see also Gould, 1971). This assumption is considered to be generally valid when the same variables from different mammalian species are studied (*e.g.*, brain weight vs. body weight, face growth vs. cranium growth, bone diameter vs. bone length). The biological interpretation in these cases is thoroughly discussed in White and Gould (1965) and Gould (1971).

Nevertheless, the similarity criterion can not be used in tree *M-D* allometry since the allometric exponent *b* in these equations is not constant among different species or even among the same species inhabiting different sites (see Table A1 and Figure 2.7). Thus, to understand better the interrelation between *a* and *b* a model based on biomechanical first principles has been formulated (Eq. 2.4b). This model accounts for the mathematical artefact in *a-b* correlation and validation against independent dataset showed a very good agreement between predicted and observed values (see Table 2.5). The model was originally formulated in order to explain the inverse relation in *a*-d** correlation (the scaling coefficients in stem biomass-diameter relationship), and information presented in Table 2.3 (see also Figures 2.3 and 2.4), shows that the model performed within reasonable levels of accuracy.

In particular, when the diameter is measured in millimetres, centimetres and metres, the model explains from 57 to 97% of the variability recorded in real *a** values (Table 2.3). The most accurate and unbiased predictions are obtained if we use the average diameter of the trees under investigation measured in meters. Despite the fact that the model gives poor predictions when diameter is measured in decimetres (Table 2.3), inspection of Figure 2.5 suggests that modelled values are within the range recorded for the empirical *a** estimates. In qualitative terms, the biomechanical model follows the same trends as the empirical data.

The flexibility of the model in modifying the values of the structural (wood density, form factor) and mechanical (safety factor) properties, allowed us to examine its performance if the 'mean' tree (*i.e.*, average wood density, average form factor, average safety factor, average diameter) is used. Quite accurate predictions of a^*-d^* relationship are obtained if the diameter is measured in millimetres and centimetres. However, the model overestimates a^* values when D is measured in meters (Table 2.4).

The effect of tree size in the model is manifested through the diameter value. As it is depicted in Table 2.3 (and Table 2.5), the model fails to capture the empirical relationship between a^*-d^* (and between a-b) when small diameters are used. This is hardly surprising, since safety factor, wood density and form factor change through ontogeny. The values used to parameterise the model based on the assumption that the aforementioned variables are invariant for trees differing in size (see Section 2.2.2.2). In addition, the values for safety factor, wood density and form factor were found in the literature and derived from open-grown trees whereas the compiled allometric pairs for a^*-d^* and a-b were computed from trees growing in dense stands.

Since the biomechanical model explains most of the variability of size-shape relationship (as manifested through a^*-d^* and a-b correlations), this implies that M_S-D and M-D equations follow an optimum trajectory, which is related to the mechanical properties of trees. If we take this leap of faith, the question immediately arises as to why trees growing at a specific site – irrespective of its geographical extent – 'select' a specific pair of a^*-d^* or a-b values and not another one. The phylogenetic effect – at least at genus and family level – contribute only partially to the solution of the problem (see Table 2.16 and Figure 2.10). If we reject the hypothesis that species 'attain' the recorded a^*-d^* or a-b pairs just at random, one can speculate that stand structure may play a key role in the observed auto-correlation. However, if that was the case, the biomass-diameter relationships (which are usually based on sample trees originating from stands with a range of different

structures) should not conform to a single power function (*i.e.*, different allometries would be expected to develope for different stands). Stand characteristics may greatly influence stem volume-diameter equations, but empirical information on *M-D* relationships do not support this (Baskerville, 1965; Bartelink, 1996; Bartelink, 1997). However, not much information was available to test this hypothesis robustly and further analysis was not possible.

The numerical correspondence between the predicted and the observed relationship of scaling parameters can not be taken as *prima facie* evidence that all the assumptions underlying the biomechanical model are valid. Nor can it be supported that universality holds true for the studied auto-correlation. This model was formulated for tree species under the assumption that individuals can not grow higher than the upper limits imposed by the biomechanical properties of their wood. Separate models have to be developed for aquatic plants or plants that belong to other taxa (*e.g.*, bryophytes).

The WBE model developed by West *et al.*, (1997), failed to predict the correlation between the scaling parameters a and b. Moreover, the average value of the compiled allometric equations for the allometric exponent (b), is statistically different (at the 95% level) from the theoretical one either using the ordinary least squares or the reduced major axis technique (Table 2.6 and Figure 2.3). The applicability of the WBE model in estimating aboveground tree biomass was examined in Section 2.3.1 and its usefulness was tested against ten datasets (Table 2.11). The WBE model failed to predict total aboveground biomass per tree in all studies as indicated by the MPD criterion. Accepting a universal value of b, implies that the ratio of the specific growth rates of M and D ($\frac{1}{M}\frac{dM}{dt}$ and $\frac{1}{D}\frac{dD}{dt}$) for different tree species growing in very diverse environments remains constant. This assumption is contrary to our understanding of ecophysiological and ecological processes. Therefore, the acceptance of a constant value of b should be viewed as tentative, and applicable only for very rough predictions of M.

2.5.2 On the 'reductionist' model

The interrelations among different dimensional quantities of trees (*D*, *H*, *V* and in effect *M*), assumes that there is a general mathematical function which should be able to capture this interdependency across different species growing under a range of environmental conditions. Since the shape of the trees is more accurately approximated within the framework provided by fractal geometry (rather than as simple Euclidean objects), a straightforward model has been formulated, based on fractal analysis, in order to describe mathematically the size-shape relation for different trees. Assuming that tree shape 'obeys' different scaling relations in response to the physical forces acting upon it (Niklas, 1992; see also Table 2.3), the dimensional interrelations of individuals are accordingly adjusted to follow global rules. For example, a specific value of b^* (exponent in *H-D*) would influence the value of b (exponent in *M-D*), in such a manner that all b-b^* pairs follow a universal trajectory imposed by common patterns.

Ideas provided by fractal analysis have been used to model tree shape, and consequently contributed to understanding the meaning of the parameter values in b-b^* empirical equation (see Sections 2.2.3.2 and 2.2.3.3). Usually, the arithmetic values of parameters in empirical regressions are not easily interpretable. However, the sum of the parameters in b-b^* relationship equals 2.6062, while fractal geometry predicts that this should be 2.5 (across different species, ages and site conditions). A fractal dimension of two would indicate that trees allocate foliage only to the periphery of the crown, while a dimension of three would imply that foliage occupies the volume of the crown (no spaces). Assuming that the empirical value is not significantly different from the theoretical one, two interconnected explanations may be given: either trees allocate photosynthates to maximize light interception and CO_2 absorption by optimising leaf and consequently branch distribution in crowns (see Zeide, 1993; Berezovskava *et al.*, 1997; Zeide, 1998) and/or the 'genetic algorithm' which defines the branching pattern of trees is essentially similar for all individuals irrespective of species. In other words, different crown architectures originate from

random processes acting upon the 'genetic algorithm' - analysis provided by Horn (2000, p.209) supports this speculation. Both hypotheses entail inherent disagreement with the biomechanical theory and suggest that new data collected either from controlled or natural environments could disentangle this controversy.

Even if the approximation provided by fractal analysis is considered to be poor, simple allometric relationships (*i.e.*, H against D) can be used to calculate upper and lower bounds on aboveground tree biomass and thus to constrain estimates of carbon storage. The combination of the biomechanical and 'reductionist' models explained 89% of the variability in M for a large compendium of different trees even though this method resulted in an overestimation, on average, by 22% (Figure 2.9). For comparison, the empirical regression developed by 223 M-D pairs yielded an average deviation between modelled and empirical values of M of 18%.

Taking into account that i) this model was based on the assumption that the fractal dimension of all trees irrespective of origin fall in between 2 and 3 and ii) there was large heterogeneity among the compiled studies used to calibrate the model, we arrived at the conclusion that this approach may result in very accurate predictions of M if additional variables are available for the calibration of Eq. (2.9) and Eq. (2.10).

Unfortunately, the 10 datasets reviewed do not provide essential information to develop testable hypothesis for disentangling the observed variability of MPD and further analysis could not take place. However, despite the moderate degree of uncertainty reported in two studies (the 5th and 7th in Table 2.12), the application of this approach may provide reasonably accurate predictions for aboveground biomass estimates if more information on the factors affecting the parameters in b-b^* and a-b relationships is available. Further research, based on empirical data, will be important to test the usefulness of this 'reductionist' approach for aboveground biomass estimation.

2.5.3 On the phylogenetic analysis

Perhaps the broadest intertaxonomic comparison that can be made for forest trees is between conifers and broadleaved species. The scaling of tree biomass is subject to the phyletic effect, since the average value of the slope (both in OLS and RMA analysis) in *M-D* relationship significantly differs between conifers and broadleaved species (Table 2.14). The scaling exponent in broadleaves is larger than in conifers (Table 2.15), but the value of the scaling constant (a) is statistically similar (at 5% level) for the two orders, when the diameter is measured in centimetres. For the allometric constant a, one should be very sceptical as to whether the interpretation of the statistical tests is correct, since the values depend on the units of measurement of the diameter (see Figure 2.1). The larger b value for broadleaves, implies that, on average, a broadleaved species would have more biomass than a conifer for the same diameter. However, a more detailed analysis on b – based on family level – indicated that no significant differences were found among 27 tree families (Figure 2.10).

To further advance the analysis of phyletic dependency of total aboveground biomass, the average biomass value was calculated for 41 genera and these values were nested within families. The results obtained indicate that more than 90% of the total variance occurred at genus and family level and only about 8% between conifers and broadleaves. Unfortunately not enough data were available to examine the variance distribution at the species level. According to Niklas (1994), this technique determines which taxonomic level obtains an appropriate magnitude of variance for subsequent scaling analysis.

Last but not least, it should be noted that conclusions drawn from any significant convergence (or divergence) in the scaling of tree size-biomass features may not support biologically sound interpretation, since judgement must be exercised on the amount of data available for each taxonomic group that was used in the analysis. In spite of the fact that no selection criterion was applied to the collected allometric equations, taxonomic groups were not equally represented in the database (Table A1) and, in effect, not much information was available to test rigorously differences

between species, genera and families. In addition, bias in the reported results originating from the violation of several statistical assumptions may lead to unsound conclusions.

3. TOWARDS THE SIMPLIFICATION OF ALLOMETRY IN BIOMASS STUDIES

3.1 INTRODUCTION

Standing tree biomass of forest ecosystems is a basic parameter in modelling several eco-physiological processes and management activities. Moreover, because of the role of forests in the global carbon (C) cycle, there is an increasing need to estimate the amount of C (or biomass since *ca* 50% is C) forests contain. Foresters and ecologists usually develop allometric empirical models which take the form

$$M = aD^b \qquad \text{Eq. (3.1)}$$

in order to relate aboveground tree biomass (M) to diameter at breast height (D). Estimation of the empirical parameters a and b is based on the destructive harvest of several trees (see Chapters 1 and 2) growing in a particular stand. This is a laborious and time consuming approach and it would be difficult to implement it at national scale. Moreover, difficulties arise, as the geographical area for which the parameters obtained are valid should be determined.

To overcome these problems several methods have been proposed in different countries. Researchers in Europe use forest inventory data and several surrogate variables (such as timber volume tables, national weighted averages for wood density, biomass expansion factors, *etc.*) in order to determine the standing forest biomass. Russian colleagues proposed a method which is based on combination of biomass regression models with the forest inventory data bank (Usol'tsev and Sal'nikov, 1998). In the USA, Pastor *et al.* (1983/1984) built generalised regressions for several tree species in order to estimate biomass values for sites where no

equation was available and recently Ter-Mikaelian and Korzukhin (1997) compiled biomass equations for 65 North American tree species.

A more synthetic approach was implemented by Brown *et al.* (1989), who fitted regressions on data that had been collected in four tropical countries. They concluded that a single equation could be applied to two of the three tropical life zones investigated. The potential for such a method was also investigated in Australia (Eamus *et al.*, 2000) and the use of a single regression over the Northern Territory was justified since the errors introduced were sufficiently small. Chave *et al.* (2001) estimated the scaling coefficients in Eq. (3.1) from raw data of tropical species reported in eight studies and subsequently applied the regression model to predict aboveground biomass of tropical rainforests in French Guiana.

More interestingly, Ketterings *et al.* (2001) suggested that values for the scaling coefficients in Eq. (3.1) could be estimated without destructive measurements on sampled trees. They supposed that a should depend on the average wood density, while b should be linearly related to the exponent which determines the *H-D* relationship at the studied site. These proposals, however, were not tested.

Remotely sensed data have also been used to estimate indirectly forest biomass through variables describing crown structure (Drake *et al.*, 2002). However, these techniques still depend on equations that relate the measured variable to tree biomass, while calibration of data is usually based on predictions made by allometric equations. Another non-destructive method was developed by Montes *et al.* (2000), who estimated the aboveground biomass of threatened species - growing in degraded woodlands – by analysing tree photographs taken from orthogonal views. They concluded that the technique developed appears to be quite reliable but only for isolated trees or individuals growing in very open stands.

As an alternative to empirical approaches, biomechanical principles of tree structure and ecophysiological models based on the fractal properties of tree branching

networks (West *et al.*, 1999), have been used to obtain estimates for the scaling exponent in Eq. (3.1). The West *et al.* (1999) fractal model (WBE hereafter) predicts that the aboveground biomass should scale against stem diameter on average with $b = 8/3$ (*i.e.* ≈ 2.67), independently of the structural and morphological characteristics of the trees under investigation. The question of whether an analysis of the existing information on *M-D* allometry provides support for this hypothesis, immediately arises.

The main objectives of this chapter are threefold:
i) To review studies that report simplified methods of tree biomass estimation.
ii) To develop generalised regressions for *Fagus* spp.
iii) To present a new simplified method for the derivation of the allometric relationship between *M* and *D*. This method is based on sampling the smallest trees only of a stand, in conjunction with information provided in the literature.

3.2 LITERATURE REVIEW

Although it is desirable to develop allometric regressions for individual sites, this method is laborious and time-consuming and imposes several technical difficulties. With these limitations (it would not be feasible to build scaling relations for every stand) and because of shortcomings emerging from the site-specific 'nature' of empirical allometries, alternative methods were developed to circumvent these problems. In the following paragraphs two different approaches for simplifying allometric studies of forest biomass are presented and their usefulness in estimating aboveground forest biomass is discussed.

3.2.1 Pooled regressions

The first method - defined as 'pooled regressions' in this thesis - was mainly developed because the extrapolation of biomass estimation equations derived from a restricted locality (or from a given species) to other sites (or to other species) is often questioned. Thus, researchers developed pooled regressions based on the destructive

harvest of several trees collected from different stands that are located in a broad geographical area (or from different species growing at a particular site). The raw data are pooled together and regression analysis is done to obtain allometric equations which are considered valid for the particular region (or set of species). It has been suggested that such equations are generally applicable over the geographical range of the aggregate data sources and provide a viable alternative when site-specific equations are unavailable and too costly to develop (Crow, 1978; Green and Grigal, 1978; Schmitt and Grigal, 1981).

Marklund (1987) reported that American workers in 1964 were the first to build biomass regressions for seven different tree species, applicable to a large area. The biomass of eight tree components was regressed against diameter and height and the equations were based on data from between 17 and 28 sample trees per species. Schmitt and Grigal (1981), developed regional biomass regressions based on data that had been collected by a number of different investigators working at several sites at New Hampshire (USA) and New Brunswick (Canada). They reported that quite accurate biomass estimations could be obtained for *Betula papyrifera* Marsh. from the pooled allometric equations, with stem diameter as the only independent variable. When height was included as a second independent variable, slightly better estimates were obtained.

More recently, Martin *et al.* (1998) destructively harvested 87 trees comprising 10 deciduous species growing in Coweeta Hydrological Laboratory in Western North Carolina in order to build interspecies pooled equations. The regressions obtained gave quite accurate predictions for the biomass values of the different tree components (stem, foliage, branches and total aboveground biomass). They also compared the pooled equations with regional regressions that had previously been developed and reported that the equations differed only slightly. However, when species-specific equations were compared with the regional regressions, considerable differences were apparent, suggesting that localised allometric relationships were preferable.

In Sweden, Marklund (1987), formulated pooled biomass functions for six tree components of Norway spruce. The equations were based on 1508 harvested trees spanning the whole country and the independent variables included diameter at breast height, total height, age of tree, crown length and radius, site index, *etc.* However, he reported that generally the biomass of the different tree components was highly correlated with the diameter and total tree height. Ben Brahim *et al.* (2000) combined raw data from four different short-rotation coppice stands in northern France, to establish a single pooled allometric equation for estimation of aboveground biomass of individual *Populus* trees. The model obtained was compared with stand specific regressions and the results indicated that the single equation performed very well for each stand.

Pooled equations have also been used in tropical forests to estimate tree biomass in regions where local regressions are not available. Brown *et al.* (1989) derived total aboveground biomass equations for individual trees as a function of life zone groups, diameter at breast height, total height and wood density. The equations developed were based on nine independent datasets, and gave estimates that were quite good for the moist and wet life zone but less accurate for the dry zone. The authors concluded that the reported equations were the best available equations as a whole - for the tropical zone - but caution should be paid in applying them to any particular region.

Chave *et al.* (2001) also applied the same approach to estimate biomass content for a lowland wet rainforest in French Guiana. The model relates M to D and was deduced from previously published data (378 trees) collected from different countries *i.e.* Brazil, Costa Rica, Puerto Rico, *etc.* Despite the fact that the estimated parameters of the scaling equation come from a relatively large number of trees, the heterogeneity of the dataset raises questions about the usefulness of the model for the particular study area. No raw data were available to validate its performance.

3.2.2 Generalised regressions

As an alternative to pooled equations, Pastor *et al.* (1983/1984) used published allometric relationships that had been developed for six North-American tree species to build a generalised equation for each tree species and component. The range of D of the sample trees was divided into five equally spaced classes and the average diameter value for each class was calculated. Subsequently, these means were used to obtain predicted M values for each size class. Finally, by combining the estimated points for all the equations, a new generalised regression having the power form of Eq. (3.1) was generated. According to the authors, this procedure ensures equal weighting of all the regressions and restricts the influence of each in the generalised regression to the diameter range for which it was developed.

To assess the variability of the generalised regressions relative to the original equations, three different statistics were used, namely the R^2 of the generalised regression, the estimate of the relative error and the mean percentage difference MPD (Section 3.3.3). It was concluded that mean differences between values predicted by the generalised regression and estimates from the original equations for total aboveground and stem biomass were within the range of error estimates reported for the individual regressions. However, for branch biomass the deviations were considerably larger.

In addition, the generalised equations for sugar maple and aspen were tested against available independent raw data sets. The results indicated an excellent prediction using the generalised regression for maple but somewhat less accurate estimations when the generalised regression for aspen was used (Pastor *et al.* 1983/1984). Finally, the authors pointed out that generalised regressions represent the average of several studies made in a large geographical area and over a wide range of diameters. Thus, it would be acceptable to implement generalised equations for predicting stand biomass in areas where it is not possible to develop original regressions.

I reviewed the available English literature to determine whether this method has subsequently been employed by other scientists. However, no further record could be found. One reason might be that not many relevant original regressions exist with which to build generalised regressions for a region.

3.3 MATERIALS AND METHODS

3.3.1 Generalised regressions for *Fagus* spp.

An approach similar to Pastor *et al.* (1983/1984) was implemented in order to obtain generalised aboveground biomass equations for beech trees. The original equations were derived from four American and three European studies (Table 3.1).

Table 3.1: Published equations for beech trees used to develop generalised allometric relationships for aboveground dry biomass using the model $M = aD^b$.

Species	*a*	*b*	R^2	*D (cm)*	*n**	*Region*	*Source*
F. grandifolia	0.2013	2.2988	n/a	3-66	29	USA	[1]
F. grandifolia	0.1958	2.2538	0.988	2-29	46	USA	[1]
F. grandifolia	0.1957	2.3916	0.994	1-60	14	USA	[1]
F. grandifolia	0.0842	2.5715	0.97	5-50	56	USA	[1]
F. sylvatica	0.0798	2.601	0.988	2-32	32	Netherlands	[2]
F. sylvatica	0.1326	2.4323	0.9983	4-35	7	Spain	[3]
F. moesiaca	0.2511	2.3485	0.9869	5-41	16	Greece	This Thesis

* Number of harvested trees. [1]: Ter-Mikaelian and Korzukhin (1997); [2]: Bartelink (1997); [3]: Santa Regina and Tarazona (2001b).

The *D* range of each equation was divided into four classes and the mean value of each class was used to derive *M* predictions from the original equations. These *M-D* pairs (28 in total) were log-transformed and a generalised regression for aboveground dry biomass of beech trees was built. This method was also applied to other tree components (stem, branches, foliage) with data points computed from the original regressions that are presented in Table 3.2.

Table 3.2: Allometric regressions for stem, branch and foliage biomass found in the literature for *Fagus* species. Coefficients *a* and *b* are for the model $M = aD^b$, except for the foliage biomass of the Dutch equation which is slightly different. R^2 denotes the coefficient of determination and *n* the number of harvested trees in each study. Species in the same order as in Table 3.1. Studies in the same order as in Table 3.1.

	a	*b*	R^2	*D (cm)*	*n*	**Region**	**Source**
Stem	0.0937	2.4700	0.9960	1-42	19	USA	[1]
	0.1381	2.2809	0.988	2-29	47	USA	[1]
	0.1155	2.4868	0.987	3-15	19	USA	[1]
	0.1067	2.3981	0.996	1-60	14	USA	[1]
	0.1515	2.2997	0.991	3-66	29	USA	[1]
	0.0762	2.523	0.93	2-32	32	Netherlands	[2]
	0.0879	2.4729	0.995	4-35	7	Spain	[3]
	0.2016	2.3426	0.9831	5-41	16	Greece	This Thesis
	a	*b*	R^2	*D*	*n*	**Region**	**Source**
Branch	0.0421	2.41	0.981	1-42	19	USA	[1]
	0.0274	2.3708	0.892	2-29	47	USA	[1]
	0.0944	1.5402	0.791	3-15	19	USA	[1]
	0.0262	2.5509	0.98	1-60	14	USA	[1]
	0.0265	2.3634	0.931	3-66	29	USA	[1]
	0.002	3.265	0.955	2-32	32	Netherlands	[2]
	0.0331	2.3678	0.9777	4-35	7	Spain	[3]
	0.0016	3.1037	0.9739	5-41	16	Greece	This Thesis
	a	*b*	R^2	*D*	*n*	**Region**	**Source**
Foliage	0.025	1.83	0.979	1-42	19	USA	[1]
	0.0233	1.6303	0.869	2-29	47	USA	[1]
	0.0216	1.8089	0.853	3-15	19	USA	[1]
	0.0183	1.9158	0.94	3-66	29	USA	[1]
	$0.375+0.0024D^{2.517}$		0.901	2-32	32	Netherlands	[2]
	0.0126	1.9953	0.978	4-35	7	Spain	[3]
	0.0152	1.6645	0.7534	5-41	16	Greece	This Thesis

[1]: Ter-Mikaelian and Korzukhin (1997); [2]: Bartelink (1997); [3]: Santa Regina and Tarazona (2001b).

Original tree biomass data, for validation of the generalised regressions, were obtained from Santa Regina and Tarazona (2001b) and from the Greek dataset (see Chapter 4). However, in order to validate the generalised regressions one would need data spanning the entire range over which the generalised equation is valid (*i.e.*, USA and Europe). To avoid confounding results, the Spanish and Greek equations were

subsequently excluded from the development of the new generalised equation - in accordance with Pastor *et al.* (1983/1984).

3.3.2 Development of the small trees sampling scheme (SSS)

The Small trees Sampling Scheme (SSS) was developed to simplify allometric analyses irrespective of tree species and forest site. Ketterings *et al.* (2001) reported that the standard deviation of trees biomass (for 5 cm D classes) was linearly related to the mean biomass of the particular D class. Accordingly, the standard error of the M per tree was smaller in lower D classes compared with the standard error of M at the upper range of D, implying that the variability around the regressed line increased in proportion to mean size. Moreover, Chave *et al.* (2001) proposed that the biomass values of the smallest trees strongly affects the values of the coefficients in the allometric relation between M and D. Motivated by these observations, I investigated the potential to develop biomass equations based on sample trees of small size, since destructive sampling of several trees spanning the entire D range of the stand under investigation is extremely time consuming.

The rationale for this approach is that additional constraints to derive a valid estimate of the 'true' allometric equation may be obtained by making use of the published information related to the compiled biomass equations. For 54 (out of the original 279) equations the D range was not available in the original articles and thus 225 regressions only were used for this method. These equations were classified into two groups, namely conifer and broadleaved species. Thus, 72 equations were used for conifers and 153 regressions for broadleaved species. A further classification was based on the D interval over which these equations hold. Compiled equations with lower and upper endpoints of the diameter interval differing by less than 2 cm were classified into the same category. Such an approach was considered to be useful since estimation of the scaling parameters in Eq. (3.1) is such that the regression line passes through the average value of $\ln D$ and $\ln M$, implying that the range of the independent variable D in this equation affects the shape of the regressed line.

The approach proposed here is based on the hypothesis that valid estimates of the scaling coefficients in Eq. (3.1) can be obtained from only two values of D and the corresponding values of M. Let (D_1, M_1) and (D_2, M_2) be the two pairs of empirical values recorded in a given stand. Based on the 225 biomass equations, D_1 and D_2 can also be used to derive the values $\hat{M}_{J,1}$ and $\hat{M}_{J,2}$ with J ranging from 1 to 225 (in reality less because of the subdivision of the dataset into two homogenous groups, namely conifers and broadleaves). For each of the 225 equations, the difference between M_1 and $\hat{M}_{J,1}$ (as well as between M_2 and $\hat{M}_{J,2}$) can easily be computed. The equation with the smallest deviation between observed M and predicted $\hat{M}$ is selected. Thus, two equations (unless the same one is selected for both cases) are available from the two pairs of the empirical values.

The selected equations may or may not be close to the 'true' regressed equation which could be developed by least-square method if several M-D pairs covering the entire D interval were available. There are nine different logical combinations that can occur for the b values, between the two selected equations and the 'true' regressed relation. These nine combinations are summarised in Table 3.3. I speculated *a priori* that the simple mathematical averages of a and b obtained from the two selected equations can be used to correctly predict M for larger diameter trees.

Table 3.3: The nine different combinations for the b values between the two selected equations and the regression curve (developed from several trees). b_1 denotes the allometric exponent obtained from the compiled equation that predicts the closest value to M_1, for D_1. b_2 denotes the allometric exponent obtained from the compiled equation that predicts the closest value to M_2, for D_2. b_{reg} is the 'true' b value that would be obtained by least square regression, if many sampled trees spanning the entire D range were available. Similar combinations apply for the allometric parameter a.

1. $b_1 = b_{reg}$ and $b_2 = b_{reg}$	6. $b_1 > b_{reg}$ and $b_2 < b_{reg}$
2. $b_1 = b_{reg}$ and $b_2 > b_{reg}$	7. $b_1 < b_{reg}$ and $b_2 = b_{reg}$
3. $b_1 = b_{reg}$ and $b_2 < b_{reg}$	8. $b_1 < b_{reg}$ and $b_2 > b_{reg}$
4. $b_1 > b_{reg}$ and $b_2 = b_{reg}$	9. $b_1 < b_{reg}$ and $b_2 < b_{reg}$
5. $b_1 > b_{reg}$ and $b_2 > b_{reg}$	

3.3.3 Statistical analysis

The ordinary least square (OLS) technique was used to derive estimates for the allometric parameters of the generalised equations on log-transformed data (Zar, 1996). To account for the inherent bias reported in logarithmic transformation (Baskerville, 1972; Beauchamp and Olson, 1973; Yandle and Wiant, 1981; Sprugel, 1983; Chapter 1) the correction factor (CF) of each equation was computed according to Sprugel (1983). In addition, to test the deviation between predictions and field data the mean percentage difference (MPD) criterion which denotes the average departure of the predicted values from the observed data, relative to the latter, was used (Pastor *et al.*, 1983/1984; Niklas, 1994).

MPD was calculated as

$$\Pi = |M - \hat{M}|/M$$

where M and $\hat{M}$ denote the real and the predicted biomass for a particular diameter, respectively and Π is the MPD.

3.4. RESULTS

3.4.1 Generalised regressions for *Fagus* spp.

The *M-D* pairs (28 in total) extracted from the seven original equations presented in Table 3.1 were logarithmically transformed in order to obtain estimates for the linear regression through the OLS method. The following generalised equation was developed for the total aboveground biomass of beech trees:

$$\ln M = 2.45(0.055)\ln D - 2.004(0.168) \qquad \text{Eq. (3.2)}$$

(R^2 = 0.987, SEE = 0.1876, standard errors in brackets, Figure 3.1A). In arithmetic scale Eq. 3.2 reads as $M = 0.1348D^{2.45}$ and it is graphically depicted in Figure 3.1B.

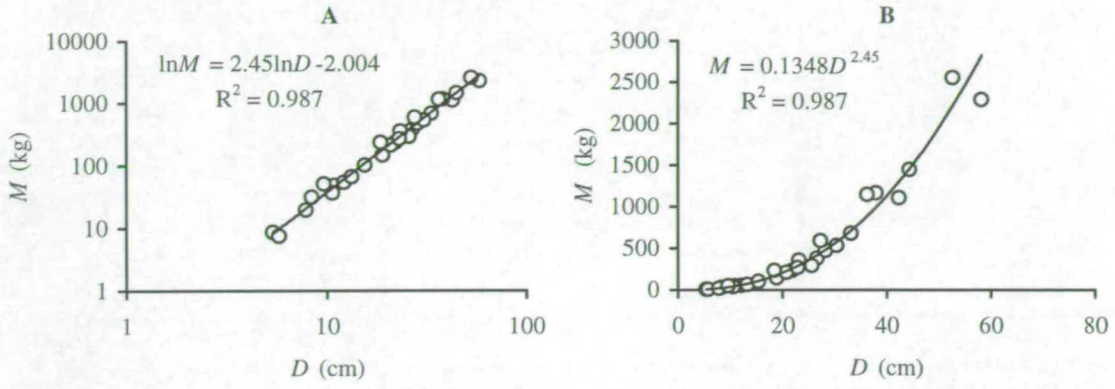

Figure 3.1: Data points (open circles) derived from seven original equations for the total dry aboveground biomass of beech species and the resulting generalised regression in **A)** logarithmic and **B)** arithmetic scale.

A very strong relationship between M and D is obtained from the generalised equation as indicated by the R^2 value, despite the fact that the individual equations originated from different sites, formulated by different researchers. It is worth noting that for the seven equations reported in Table 3.1, the coefficient a varied between 0.0798 and 0.2511 and the coefficient b between 2.2538 and 2.601. Despite these large ranges of the coefficients, all predicted points of M essentially collapsed onto the same curve. This is likely to be because of the correlation between a and b such that when a is large b is small (Figure 3.2A). A significant relationship is obtained when a is plotted against b for stem and branches allometries (Figure 3.2B, C) but a very weak correlation is obtained for foliage allometries (Figure 3.2D). Pastor *et al.* (1983/1984), also reported very high correlations in M-D generalised regressions for several tree species that were investigated.

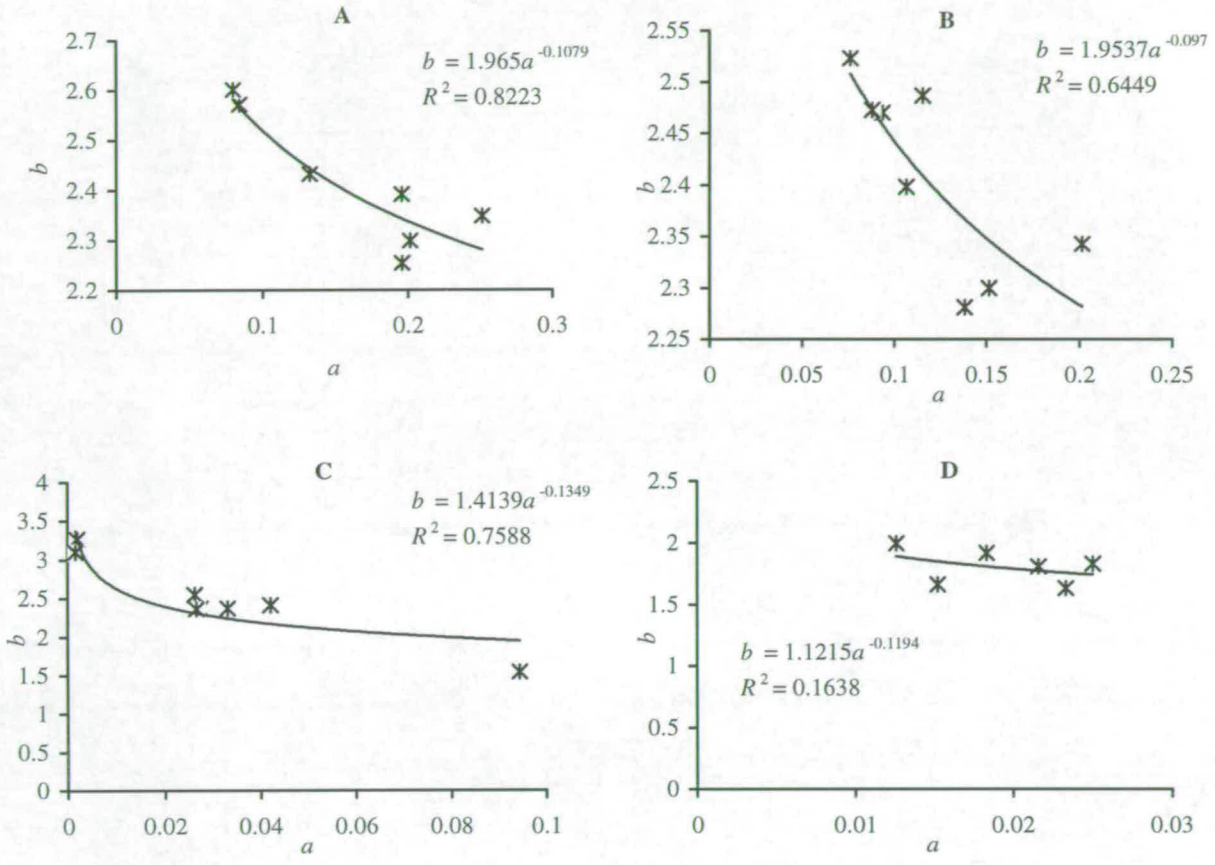

Figure 3.2: Correlation between the allometric coefficients of *Fagus* spp. equations for **A)** total, **B)** stem, **C)** branch and **D)** foliage components (data from Table 3.1 & Table 3.2).

Generalised equations for stem, branches and foliage mass have also been computed, based on data points from the original regressions compiled in Table 3.2. Statistical parameters for the developed equations are presented in Table 3.5 and the regressions are depicted in Figure 3.3.

To assess the variability of the generalised equations relative to the original regressions, the MPD between predictions made by the generalised and the original equations was calculated and presented in Table 3.5 for the different biomass

components. Total and stem MPD for beech species is within the range of the percentage difference reported by Pastor *et al.*, (1983/1984), (7.2-39%) but no comparisons can be made for deviations in leaf biomass since such equations were not presented in the American study. MPD for branch prediction is very high (58%) but Pastor *et al.* (1983/1984) also reported high MPD values for generalised branch equations for red maple, sugar maple and yellow birch (47.8-77.2%).

Table 3.4: Generalised equations for *Fagus* species and different tree components. The equations are in logarithmic form $\ln Y = \ln a + b \ln D$ where Y is the total, or stem, or branch, or foliage biomass. Data points were derived from the equations presented in Table 3.1 and Table 3.2. SEE stands for the standard error of estimate, CF is the correction factor for logarithmic bias and MPD, the mean percentage difference between observed and predicted values.

Component	ln*a*	*b*	*D* (cm)	R^2	SEE	CF	MPD(%)
Total	-2.004	2.45	1-66	0.987	0.1876	1.01	14.86
Stem	-2.027	2.3594	1-66	0.995	0.102	1.00	12.67
Branches	-3.823	2.4208	1-66	0.786	0.6036	1.19	58.11
Foliage	-3.979	1.8169	1-66	0.8582	0.3628	1.06	32.29

The generalised equation for branch biomass has given the lowest R^2 (0.78) while for the other tree components better correlations are found (Table 3.4). According to Pastor *et al.* (1983/1984), the R^2 of the generalised regression applies to the generated points only and indicates the amount of variation of the predictions by the original regressions accounted for by the generalised regressions. They reported higher R^2 values for all tree species and tree components than the ones presented here. The small values of correction factors (CF) reported in Table 3.4 for all tree components indicate that unbiased estimations are expected if we simply apply the antilog function of the logarithmic predictions in order to obtain corresponding readings in arithmetic units.

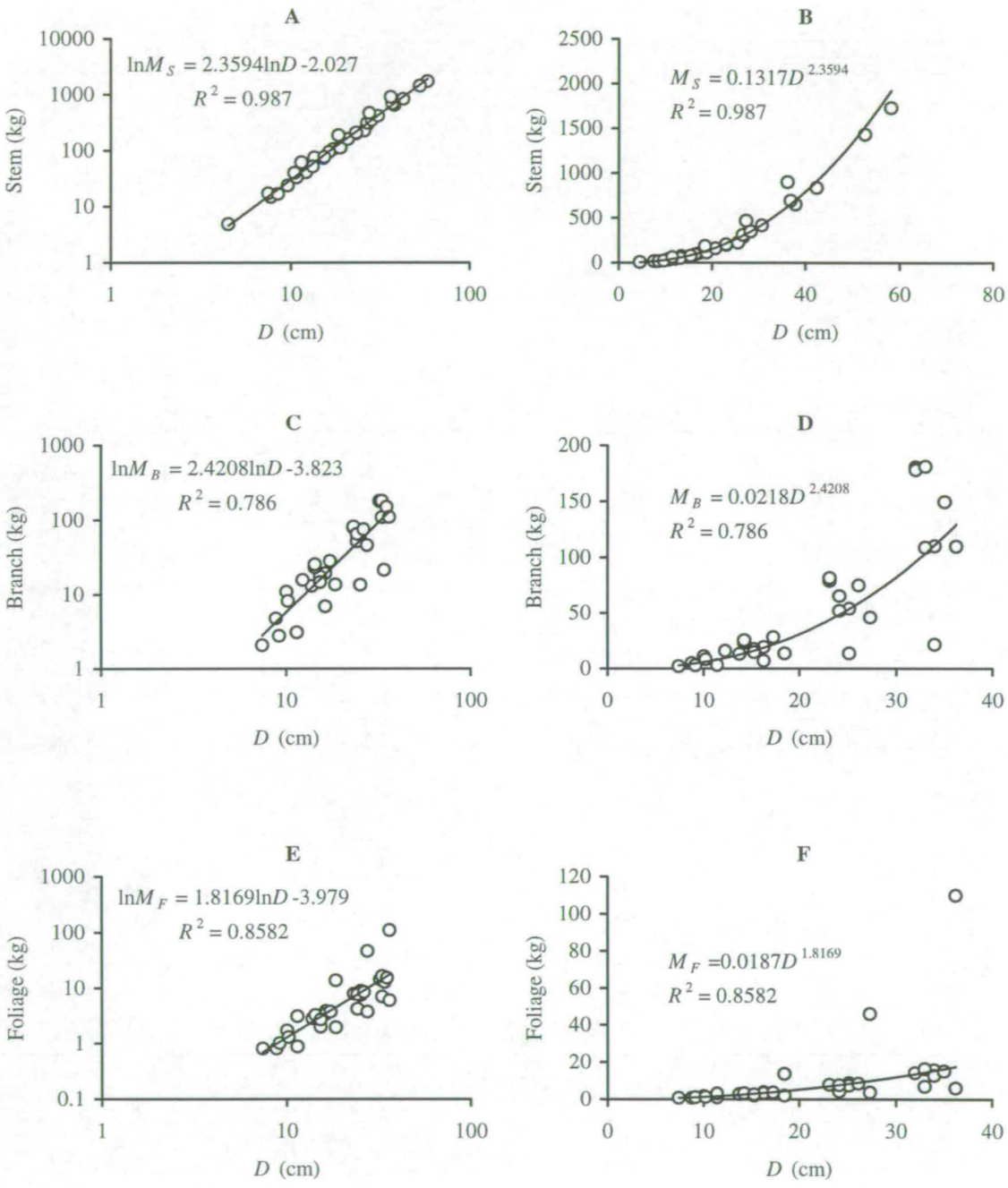

Figure 3.3: Generalised allometric equations for stem (**A-B**), branches (**C-D**), and foliage (**E-F**) biomass for *Fagus* trees in logarithmic (left panels) and arithmetic scale (right panels).

Raw biomass data reported in two studies for different components of beech trees were used in order to test the applicability of the generalised regressions to stand scale. The first dataset was derived from a Spanish stand (Santa Regina and Tarazona, 2001b) and the second from a Greek forest (see Chapter 4). Applying the same procedure as before - but excluding the Spanish and Greek equations - generalised biomass equations were derived for the different tree components.

The new generalised equation for aboveground tree biomass takes the form:

$$\ln M = 2.456(0.05)\ln D - 2.073(0.156) \qquad \text{Eq. (3.3)}$$

($R^2 = 0.992$, SEE = 0.1551, standard errors in brackets). This regression very closely predicted biomass values for the Spanish dataset and there was virtually no difference between estimations made by the original and generalised regression (Figure 3.4A). On the contrary, the generalised equation did not accurately fit the data collected from the Greek stand (Figure 3.4B).

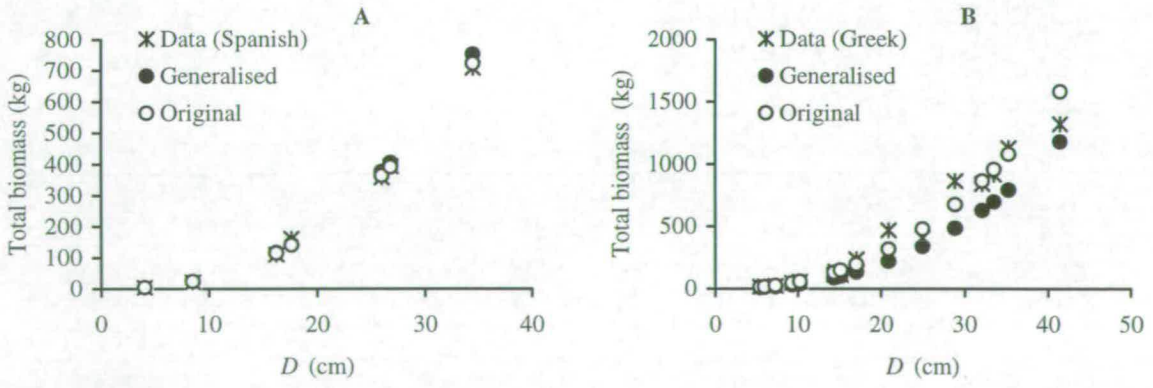

Figure 3.4: Predicted values of *M* from the new generalised (Eq. 3.3) and original equation for the **A)** Spanish and **B)** Greek dataset. Raw data are also shown.

For the original Greek equation MPD = 13.54%, while the new generalised regression yielded a MPD = 31.17% which is relatively high but within the range (10-35%) reported for original regressions developed from field data (Pastor *et al.*, 1983/1984). In addition, the pooled data from the two datasets were used to validate the generalised relationship and MPD equalled 23.82% (Figure 3.5A), which is a rather accurate estimate, considering that no adjustments were introduced to take into account different anatomical and morphological characteristics of the harvested trees (stand structure, wood density, tree age, tree height, *etc.*).

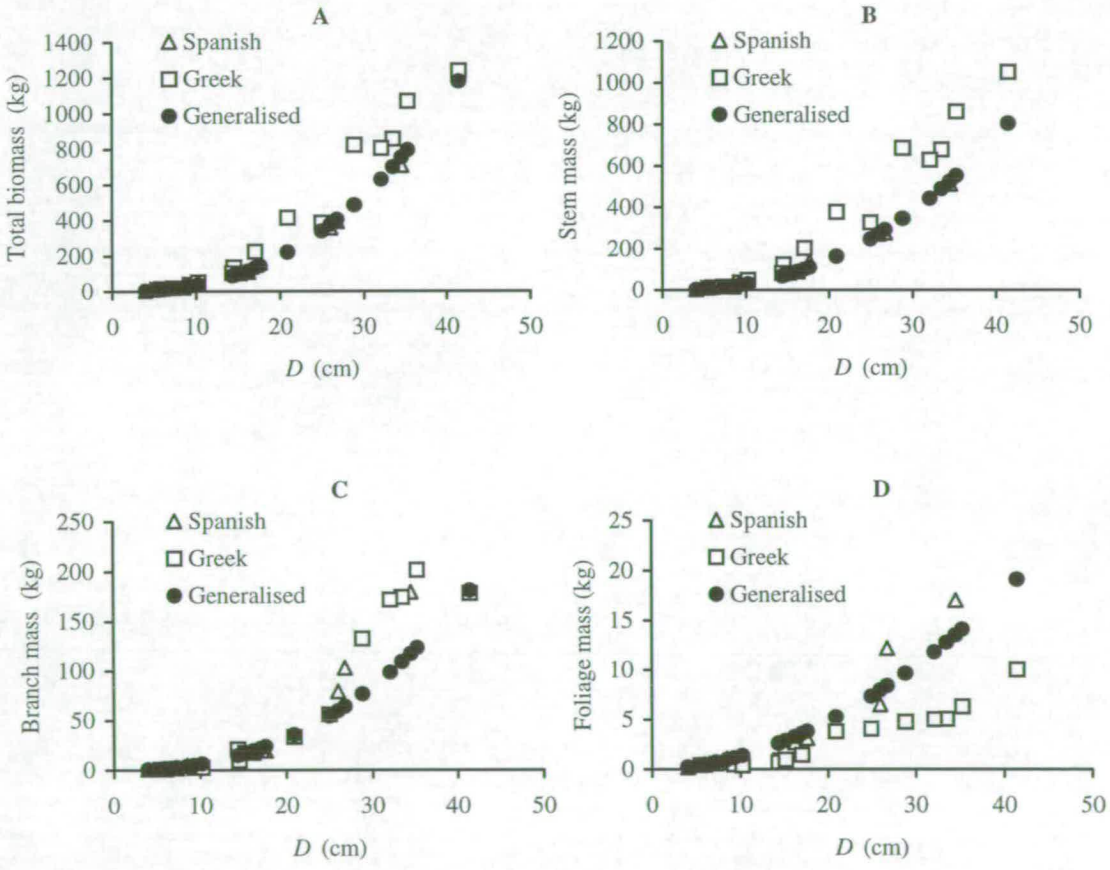

Figure 3.5: Validation of the new generalised biomass equations for **A)** total aboveground, **B)** stem, **C)** branches, and **D)** foliage compartments for *Fagus* species. Pooled data are superimposed.

The value of MPD between predicted and pooled stem biomass data was less than 27% (Figure 3.5B), and was about 40% for the pooled branch biomass dataset (Figure 3.5C). Generalised regression for foliage mass failed to predict the Greek raw data (MPD = 123%) but reasonably good estimations for the Spanish stand were obtained (MPD = 20%; Figure 3.5D). The large deviation for the Greek dataset may be explained by the fact that foliage mass is strongly related to sapwood area rather than to D as documented in several studies (Shinozaki *et al.*, 1964; Waring *et al.*, 1983; Meadows and Hodges, 2002; to name but a few). However, since no regression was found in the literature that relates sapwood area to leaf biomass for beech trees (see Bartelink, 1997 as an exception), a generalised equation for these variables could not be developed. For the pooled foliage dataset MPD = 92% (Figure 3.5D).

3.4.2 Small tree Sampling Scheme (SSS)

The main practical application of SSS is apparent: to have the allometric relationship for the entire D range one has to sample only small trees. All other predictions are based on these data. To illustrate the SSS approach, the dataset by Woods *et al.* (1991) on *Picea mariana* (Mill.) was used (Table 3.5). The method includes the following steps:

1. Identify the D range of the given dataset, namely $2.9 < D < 23$ cm. Thus, all the equations developed for coniferous species with lower endpoint of the D interval between 0-5 cm (and with upper endpoint of D interval between 21-25 cm) are selected for the next step. In this example, six equations out of 67 (compiled for coniferous species) were selected.

2. Choose the two smallest trees, namely $D_1 = 2.9$ cm, with $M_1 = 0.95$ kg and $D_2 = 4.1$ cm, with $M_2 = 3.54$ kg. Calculate the predicted $\hat{M}_{J,1}$ and $\hat{M}_{J,2}$ values for the two diameters D_1 and D_2 based on the six selected relations and find the equation that

correspond to the smallest difference between the real and the predicted biomass values for each diameter.

3. Calculate the average value of a and b parameters obtained from the two equations and apply the computed averages in Eq. (3.1) to estimate M for the entire D range.

Table 3.5: Woods *et al.* (1991) raw data and predictions made by the regression method (R), the SSS model (SSS) and the power function (P) based on two points only. The mean percentage difference (*MPD*) between predicted and observed M value for each tree is also reported. MPDREG, MPDSSS and MPDP stand for the MPD calculated for the regression technique, for the SSS model and the power function, respectively. ID refers to individual trees.

ID	D (cm)	M (kg)	R (kg)	SSS (kg)	P (kg)	MPDREG	MPDSSS	MPDP
1	2.9	0.95	1.30672	1.34071	0.95	36%	39%	0%
2	4.1	3.54	2.95598	3.03982	3.15	16%	14%	10%
3	4.1	5.25	2.95598	3.03982	3.15	43%	42%	39%
4	4.4	3.28	3.4914	3.59211	4.02	6%	9%	22%
5	4.9	3.72	4.4998	4.63288	5.82	20%	24%	56%
6	5.1	4.38	4.94482	5.09241	6.69	12%	16%	52%
7	5.5	6.24	5.9082	6.08758	8.68	5%	2%	39%
8	5.7	6.17	6.42723	6.62393	9.81	4%	7%	58%
9	6.9	8.86	10.0839	10.4056	18.96	13%	17%	113%
10	8.2	14.60	15.1478	15.6489	34.37	3%	7%	135%
11	9.1	16.96	19.3628	20.0171	49.21	14%	17%	190%
12	9.2	19.91	19.8682	20.541	51.09	0.2%	3%	156%
13	11	35.58	30.2764	31.3386	94.58	14%	11%	165%
14	11	31.18	30.2764	31.3386	94.58	2%	0.4%	203%
15	11.5	43.37	33.6212	34.811	110.24	22%	19%	154%

Table 3.5: (*continued*)

ID	*D* (cm)	*M* (kg)	R (kg)	SSS (kg)	P (kg)	MPDREG	MPDSSS	MPDP
16	12.1	32.54	37.9038	39.2583	131.35	16%	20%	303%
17	12.7	45.65	42.4846	44.0169	155.19	6%	3%	239%
18	14.1	53.86	54.3618	56.3613	222.52	0.9%	4%	310%
19	14.3	60.97	56.1971	58.2695	233.58	7%	4%	283%
20	14.4	52.10	57.1279	59.2374	239.26	9%	13%	360%
21	15.6	59.78	68.9916	71.5771	315.25	15%	19%	430%
22	15.6	62.14	68.9916	71.5771	315.25	11%	15%	407%
23	16.4	70.46	77.6242	80.5598	374.54	10%	14%	431%
24	18.1	133.18	97.9436	101.714	526.137	26%	23%	295%
25	18.9	128.70	108.456	112.663	610.692	15%	125	374%
26	19	114.13	109.814	114.078	621.898	3%	0.05%	444%
27	19.6	114.82	118.165	122.778	692.223	2%	65	502%
28	20.2	128.89	126.87	131.849	768.015	1%	25	495%
29	20.8	104.98	135.934	141.296	849.518	29%	345	709%
30	22.8	137.07	168.78	175.544	1165.63	23%	285	750%
31	23	204.60	172.291	179.206	1201.25	15%	12%	487%
					Average	***13.4%***	***14.5%***	***265%***

In Table 3.5, biomass predictions calculated with the SSS method (hereafter called SSS equation) are compared with raw data (reported in Woods *et al.* 1991) and the corresponding regressed values (see also Figure 3.6). A power function has also been fitted to the two pairs of *M-D* data. The regression and the power functions were fitted with the least square technique using 31 and 2 pairs of *M-D* values, respectively. No correction factor was introduced in order to eliminate the inherent bias (see Section 3.3.3). The SSS equation was based on 2 points of *M-D* values (the same as the power function) following steps 1 through 3.

The mean percentage difference is quite similar for the regressed and SSS values (13% and 14% respectively, Table 3.5) indicating that if both functions were applied to the entire stand, the same standard error arising from the prediction equations would be obtained (Figure 3.6). As expected, the power function based on two pairs only does not provide accurate predictions (Table 3.5). Two other pairs of *M-D* were used to test the applicability of the SSS method. If $D_1 = 2.9$ cm with $M_1 = 0.95$ kg and $D_2 = 4.1$ cm with $M_1 = 5.25$ kg the modelled value of MPD is about 14% for the SSS equation, indicating that biomass variability of small trees (compare with *M-D* values in step 2) may not largely affect the results obtained by this method.

It is expected that a reasonable number of sampled trees (not less than 3) for each diameter would give better results. Mean values of *M-D* variables were available for the 4 and 5 cm diameter classes, based on 4 and 3 sampled trees, respectively. These values were implemented in SSS and the computed MPD was equal to 16% (close to 13% obtained with the regression method based on 31 trees). The SSS method was then applied to the 10 studies presented in Table 2.9, based on the two *M-D* pairs with minimum difference in *D*. The potential of using the biomasses of the two smallest trees in each study was tested and the summarised results are presented in Table 3.6. The MPD values for the regression, the SSS method and the power function in each dataset are reported; the diameters of the two smallest trees D_1, D_2 used in the SSS equation and for calibrating the power function are given in the last two columns. It should be noted that in the 5th and 6th datasets the two trees with the smallest *D* differed by 15 and 4 cm respectively, and one of the assumptions in SSS model is violated. Thus, using trees that differ less than 2 cm in *D*, seems to improve the predictions (Table 3.6). In the 10th study, the raw data were collected from various tropical species with different wood anatomy and crown architecture and it is speculated that tree-to-tree biomass variability would be large, for a given *D* as evident from the MPDREG value.

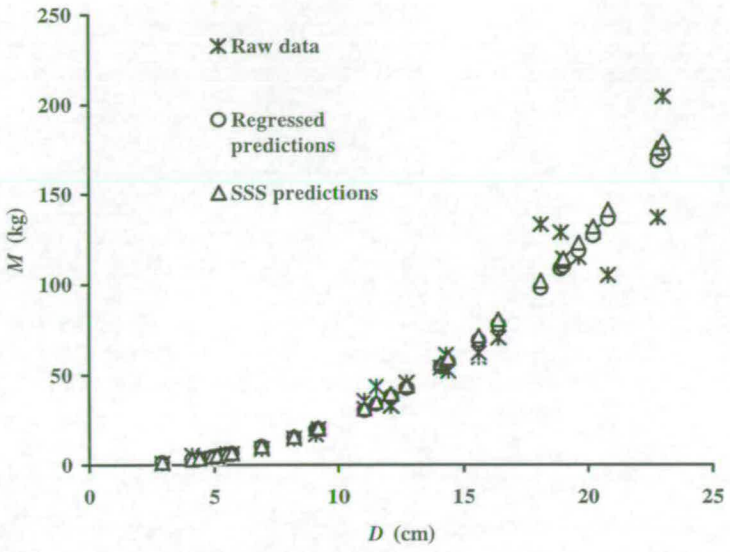

Figure 3.6: Predicted values for regression (based on 31 data pairs) and SSS equation (based on 2 data pairs). Raw data reported in Woods *et al.* (1991) were used in this graph. See also Table 3.5.

Thus, two *D* classes were used for the smallest five trees spanning from 7.6 to 9.9 cm; the SSS method was applied to the average *D* and *M* values per diameter class and quite reliable biomass estimates are obtained for the entire *D* interval as indicated by the comparison of the MPD between the regressed and SSS equations presented in Table 3.6. Beside using the MPD criterion, the obtained equations for each study were also plotted and a visual analysis illustrated no evidence of systematic under – or over – estimation across ten different datasets (Figure 3.7). In the second, fifth and tenth study, predictions from SSS equation are slightly larger than the regressed estimations (Figure 3.7B, E, J). On the other hand in the 3rd, 4th, 6th, 7th, and 8th dataset SSS predictions are somewhat lower than the predictions from OLS regression, (Figure 3.7C, D, F, G, H) while no difference is depicted for the first and ninth study (Figure 3.7A, I).

To resume: Based on sampling trees that belong to neighbouring diameter classes (differences less than 3 cm), and following steps 1 through 3, one can obtain the

allometric coefficients for Eq. (3.1). Applying this equation to the entire D range of the stand under investigation, quite reliable M predictions are computed. The larger the size of the sacrificed trees, the more individuals to be harvested per each D.

Table 3.6: Summary of the mean percentage difference, MPD, values for three different models (MPDREG for the regression, MPDSSS for the SSS model and MPDP for the power function) computed for 10 studies. The diameters of the smallest trees used in calibrating the SSS model and the power function are reported in the last two columns. Study numbers correspond to Table 2.9.

Study	MPDREG	MPDSSS	MPDP	D_1 (cm)	D_2(cm)
[1]	0.1339	0.1452	2.6530	2.9	4.1
[2]	0.0862	0.0905	0.1468	5.8	8.5
[3]	0.1533	0.1838	0.7650	0.9	1.2
[4]	0.0947	0.0928	0.0891	6.3	9.8
[5]	0.1303	0.2104	0.6116	17.5	19.1
[6]	0.0552	0.0784	1.2456	16.2	17.6
[7]	0.1091	0.182	0.4812	7.1	8.9
[8]	0.0993	0.1096	1.5823	8.77	8.8
[9]	0.0734	0.0743	0.2829	13.4	17.2
[10]	0.2865	0.3159	0.3474	7.8	9.8

Small trees yield comparably accurate biomass predictions for the entire D range but it should be noted that trees with $D < 1$ cm may provide unreliable estimates as adequate information does not exist in the dataset of the compiled equations for these D classes. Finally, the D range of trees whose M is to be estimated with the SSS, is the most important criterion in selecting the appropriate compiled equations – *i.e.*, equations developed for diameter range similar to D.

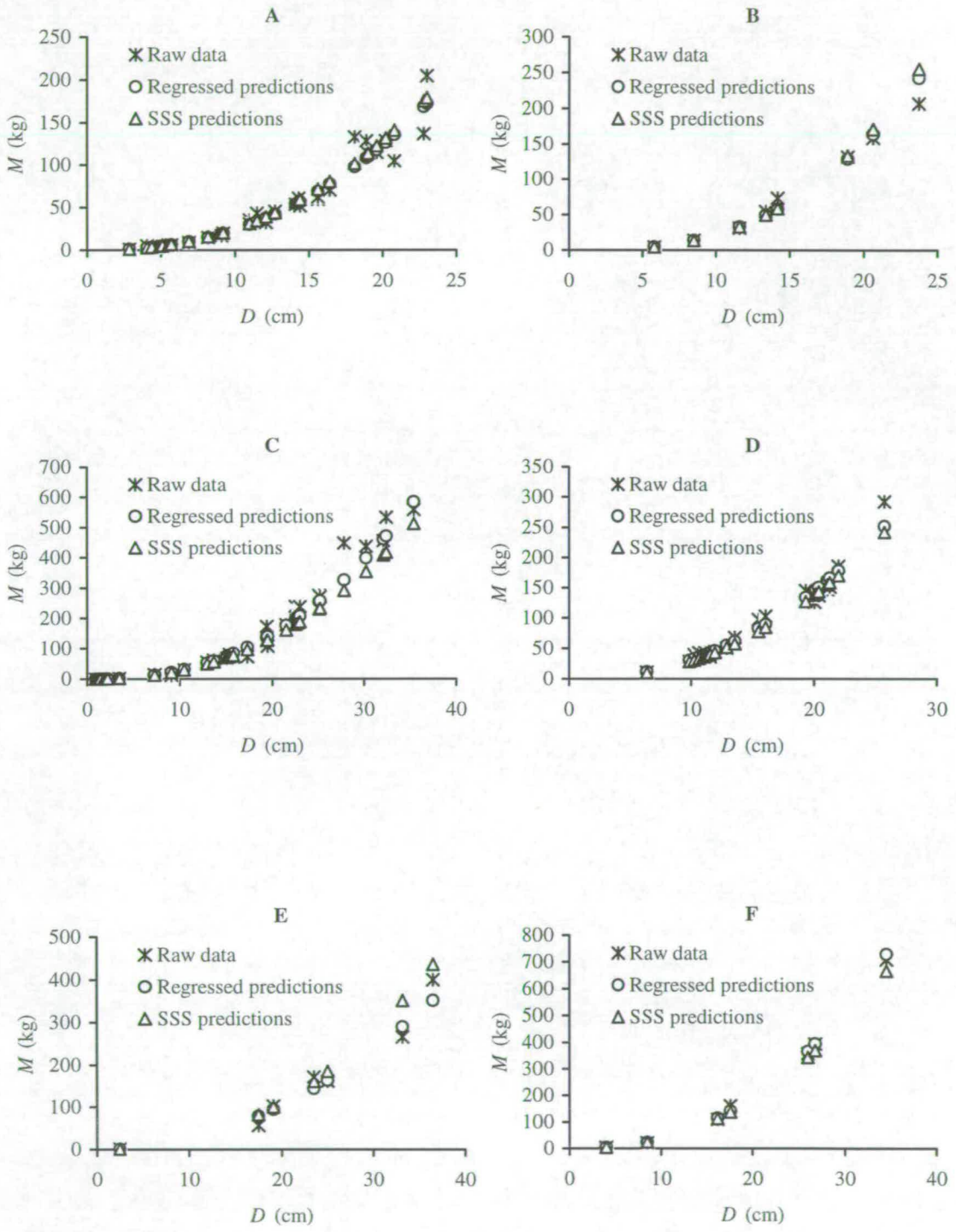

Figure 3.7: (*continued*)

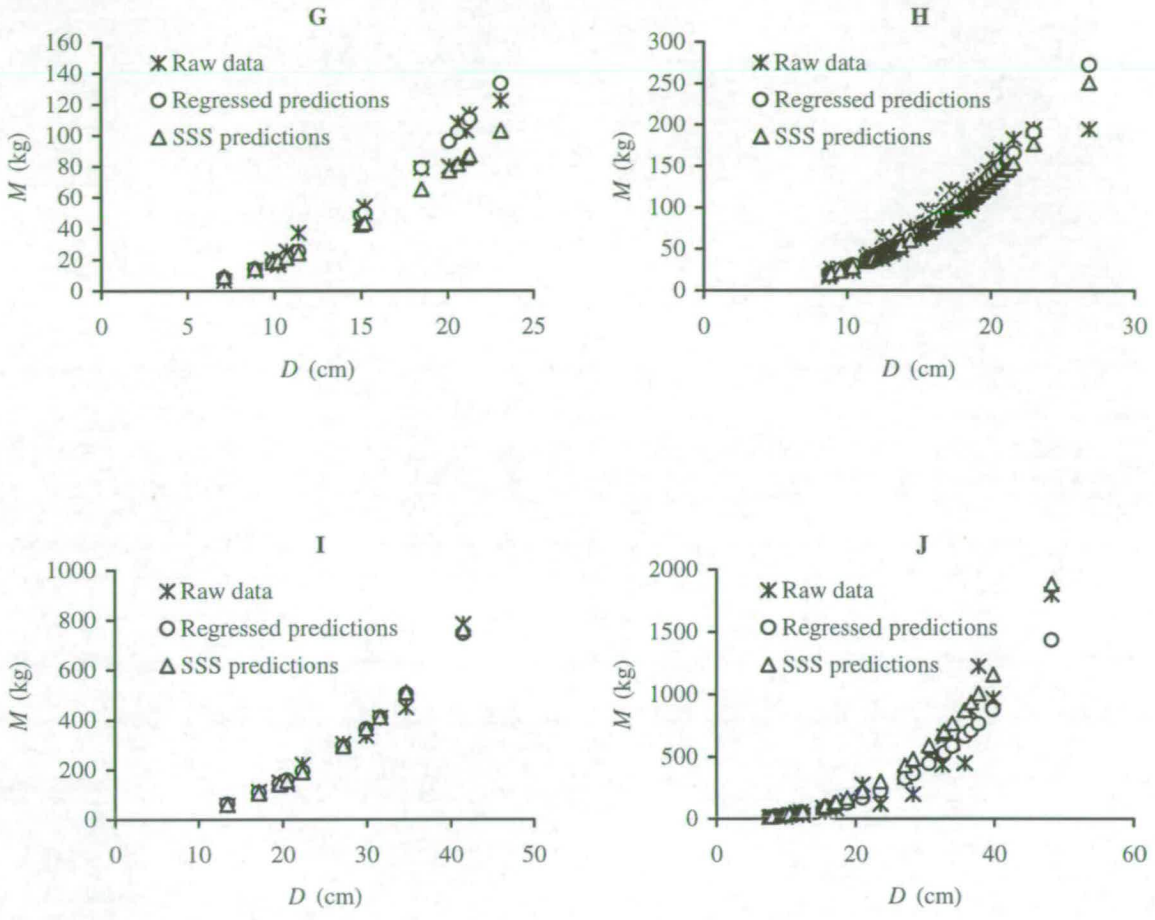

Figure 3.7: Predicted values for regression and SSS equation. Raw data derived from **A)** Woods *et al.* (1991); **B)** Gower (pers. comm.); **C)** Woods *et al.* (1991); **D)** Lim (1979); **E)** Santa Regina and Tarazona (2001a); **F)** Santa Regina and Tarazona (2001b); **G)** Jokela *et al.* (1981); **H)** Menguzzato and Tabacchi (1986); **I)** Cerny *et al.* (2000); **J)** Ketterings *et al.* (2001) were used in this graph. For more information on each study see Table 2.9.

3.5 DISCUSSION

Simplification methods for the estimation of forest aboveground biomass fall into two categories according to the spatial scale at which they are to be applied:

1) The pooled regressions and the generalised equations seem to provide reliable estimates when *M* values are needed for a broad geographical area (regional or continental scale). Under- and over- estimates of particular stands may cancel out when the aforementioned models are implemented on a large area and thus quite accurate *M* estimates may be obtained. However, extensive validation of the first two models did not take place since it is extremely hard to find appropriate raw data to test these methods under statistically sound principles.

2) At the stand (or site) scale, the SSS method gave quite accurate estimates of the field data (Table 3.6). In the last three Sections of this Chapter a more detailed discussion for each of the simplifying methods described above will be presented.

3.5.1 On pooled regressions

When site - specific regressions are not available for estimating tree biomass, researchers tend to use pooled allometric relationships that were formulated from data originating from broader regions. This method has been applied in boreal, temperate and tropical ecosystems, for predicting forest biomass per unit area, and several investigators have reported that the predicted values fell within acceptable levels of accuracy (Marklund, 1987; Nelson *et al.,* 1999; Ben Brahim *et al.,* 2000; Eamus *et al.*, 2000; Chave *et al.,* 2001). However, two main practical implications may restrict the usefulness of this method.

Firstly, the limit of the geographical area – or the habitat - for which the pooled equation is valid is usually not mentioned. For instance, Brown *et al.* (1989) stated

'We feel that the equations reported in this paper are the best available for the tropics as a whole...'

but analyses made on independent empirical data, presented in Chave *et al.* (2001), verified that these models did not provide accurate predictions. In addition, Chambers *et al.* (2000) developed a model for central Amazon based on 315 trees and compared it with four equations built for tropical forests; they reported that the predictions of the wet forest model (Brown, 1997) differed substantially from the central Amazon regression. Thus, further investigation based on much more data is needed in order to assess the usefulness of pooled equations in biomass studies.

Secondly, improved predictions from the pooled equations are obtained when several independent variables are introduced in the model (Marklund, 1987; Nelson *et al.*, 1999; Eamus *et al.*, 2000) rather than D and/or H alone. However, these 'extra' variables are not usually recorded during forest inventories, and thus accuracy of predictions may be questioned. Moreover, methodological differences among studies and inadequate number of sampled trees [the pooled data are not considered to be representative of the population of interest- Marklund's (1987) dataset may not be an exception], raise statistically sound objections. In effect, generalised equations may be more accurate in predicting M values over a large area than estimations provided by pooled regressions. A final conclusion is that local biomass equations based on trees from the individual stands will certainly be more reliable than pooled equations, which are intended for a more general use.

3.5.2 On generalised equations

Published regressions for beech species were found in the literature and generalised equations for different tree components of *Fagus* species were subsequently developed. Pastor *et al.* (1983/1984) pointed out that generalised equations may readily be formulated for species and regions other than the ones that they had studied. However, scanning the literature it seems that researchers involved in biomass studies have not extensively applied this method.

In this chapter, generalised regressions for *Fagus* species were built, based on four American and three European studies. The developed regressions accounted for more than 98% of the variation in predicted values by the original equations for total and stem biomass, but lower R^2 estimates were obtained for branch and foliage biomass (Table 3.4). Mean percentage difference for branch mass amounted to 58.11% and Pastor *et al.* (1983/1984) attributed this large deviation to the difficulties in separating stem and branches in broadleaved trees. Pooled raw data harvested in a Greek and a Spanish stand were used in order to test the performance of the generalised equations. Large deviations between predicted and observed values were found for branch and foliage compartments, but reasonably accurate predictions were made for stem and total aboveground biomass (Figure 3.5).

The generalised regressions presented in Table 3.4 represent the average equations for beech trees since they were formulated from different site-specific allometric relationships. Using these 'representative' equations may prove to be useful in predicting biomass values at a regional or continental scale and the approach is straightforward since the driving variable, D, is usually recorded in forest inventories of different countries.

However, the level of uncertainty inherent in estimations made by generalised regressions is not easily defined. Standard errors of parameters refer to the accuracy of the generalised regressions in relation to original predictions and not against field observations. This may be the reason for the excellent prediction for total aboveground and stem biomass as opposed to branch and foliage mass. Using other tree variables (height, crown radius, *etc.*) could increase the performance of the models for estimating crown mass. Diameter alone is not a good predictive variable for branch and foliage biomass and as a consequence generalised estimations may be biased in predicting these values. On the other hand, total aboveground and stem mass are highly related to D and accurate estimates are expected when applying generalised regressions over a large geographical area.

3.5.3 On the SSS method

The development of a new method (SSS), by which the allometric relationship between M and D for the entire D range can be obtained from destructively sampling of small trees, together with information provided in published equations, has been outlined in Section 3.4.2 and tested. Raw data of D and corresponding M from 10 studies were used to test the applicability of the SSS approach. Results presented in Table 3.6 indicate that SSS equation provides a good balance of quite accurate biomass predictions and small data requirements. This method is based on the destructive sampling of small trees with D values that differ by no more than 3 cm. If larger trees are used then the number of sampled individuals per D class should be increased to account for increased variability in M at larger tree sizes. A procedure for the estimation of the standard error in SSS is not currently available, but it is clear (see Table 3.6) that is likely to be close to the standard error obtained from the standard regression equation and consequently falls within acceptable limits. Moreover, the accumulated error in predicting M from D tends to be smaller for sites with a large number of trees (see Woods *et al.* 1991), implying that the implementation of the SSS allometric equation at the stand scale may result in quite accurate predictions for aboveground biomass. Since no selection criteria were used in selecting the data to validate the SSS method - *i.e.* the raw data obtained from the 10 studies (Table 2.9) were randomly chosen – the method seems to be broad applicable. If this holds true, then the SSS approach may apply to other tree variables (*i.e.,* stem biomass, branch biomass, leaf biomass, *etc.*) and to other life forms or natural phenomena that obey scaling laws.

4. ALLOMETRIC RELATIONSHIPS FOR BEECH (*Fagus moesiaca* Cz.) TREES AND STAND BIOMASS ESTIMATION: THE CASE STUDY OF NAOUSA FOREST, NORTHERN GREECE

4.1 INTRODUCTION

The United Nations Framework Convention on Climate Change and in particular the Kyoto Protocol recognise the importance of carbon stocks and the need to monitor, preserve and enhance terrestrial carbon stores. Terrestrial biotic carbon stores are difficult to assess and most current estimates are subject to considerable uncertainty (Clark *et al.*, 2001). As biomass (*i.e.*, the total over-dried biological material or mass in a given area at a given time) is approximately 50% carbon, changes in the total biomass through time are important from local to global scales. Forest biomass changes as a result of succession; direct human activities such as silviculture, harvesting and clearing for conversion to non-forest use; natural disturbances caused by wildfire and/or insect outbreaks; and changes in climate and atmospheric pollutants. Thus, biomass is a useful measure for assessing changes in forest structure, and is a useful measure for comparing structural and functional attributes of forest ecosystems across a wide range of environmental conditions (Brown *et al.*, 1999).

Direct determination of forest biomass by destructive harvest of all trees growing in a specific area is a time consuming and labour intensive procedure and has rarely been implemented (Brown and Iverson, 1992). In statistical terms, biased estimates are expected from this method if the results are extrapolated to an area larger than the sampled plots. To circumvent this problem, the morphometric characteristics of destructively sampled trees are measured and subsequently regression equations are fitted to these datasets. To obtain unbiased estimates for the biomass values, the

harvested trees should have a similar size range as the trees the biomass of which is to be predicted. This method has been applied to either one species (*e.g.*, Bartelink, 1996; Bartelink, 1997) or to different tree species growing at the same site (*e.g.*, Martin *et al.*, 1998). Scaling equations that relate different morphometric parameters for trees may also provide theoretical insights into understanding the response of individuals to physical forces acting upon them through biomechanical principles (Niklas, 1992; Niklas, 1994; Chapter 2).

Despite the fact that a voluminous number of allometric relationships has been developed for different tree species growing in several European countries (see European database, Chapter 1), to the best of my knowledge only one paper reports regression equations that have been built for trees growing in Northern Greece (Alifragis *et al.*, 2001) for Allepo pine. However, it would not be ecologically and statistically sound to implement empirical equations for beech trees developed elsewhere – *e.g.*, Nihlgard (1972) in Sweden; Bartelink (1997) in Holland; Santa Regina and Tarazona (2001) in Spain – to a forest in Greece. As a reference point it should be noted that Parde (1980) reviewed historical and methodological aspects of forest biomass studies and Cannell (1982) compiled data on biomass production from studies conducted throughout the world.

In this Chapter an attempt to develop scaling relationships for the estimation of aboveground tree biomass for beech trees growing in Vermio Mountain, Northern Greece, is presented. In addition, inferences about the biomechanical properties of the sampled trees are analysed through investigation of the deviation between theoretical and empirical values of the scaling exponents. The raw data will also be used to validate the SSS method presented in Chapter 3. Finally, the allometric relationships obtained will be applied to estimate the dry biomass of the investigated beech forest at the stand scale.

4.2 MATERIALS AND METHODS

4.2.1 Study area

The Vermio Mountain is situated in the central part of Northern Greece, about 80 km west of Thessaloniki, with a north-south orientation. The east slopes are influenced by pluvial aerial masses originating from the Aegean Sea resulting in highly productive ecosystems in comparison to western sites. The forest studied (40°32N, 21°58E) is located on the eastern slopes of Vermio Mountain, spanning from 380 to 2052 m above sea level and belongs to the Municipality of Naousa town. Several plant species (*Pinus nigra, Abies borissi-regis, Castanea sativa, Ilex aquifolium, Juniperus* sp., *Quercus* sp., *Salix* sp., *Populus* sp., *Platanus* sp, *Acer* sp., *Fraxinus* sp., *Buxus sempervirens, Cornus* sp., *Prunus* sp., *Rubus* sp., *etc*) can be found in this ecosystem corresponding to the variety of site conditions. The climate of the forest can be classified as temperate Mediterranean with rainy winters and warm summers and, according to Stefanidis (1991), the total annual amount of rainfall is 1500 mm. Minimum rainfall occurs during the July-August period, but the atmosphere is not totally dry because of the nearby archipelagos.

Naturally regenerated, pure beech (*Fagus moesiaca* Cz.) stands occupy a total area of 2121 ha, stretching from 900 m to 1900 m covering a range of different topographical characteristics (see Table 4.1). The disturbed history of the forest (clearcut fellings during the 19th century and several fire events during World War, II), it is usual to encounter cohorts of trees within stands that belong to different age-classes and consequently to different size-class.

4.2.2 Tree scale data

Sixteen trees were harvested from the stands described in Table 4.1 for the parameterisation of the allometric equations. The range of diameters at breast height (*D*) of the felled trees spanned from 5.19 to 40.6 cm so as to represent the diameter distribution reported in the forest management plan.

Table 4.1: Structural characteristics of 4 stands across an elevation gradient as modified from Stefanidis (1991). MAI denotes the mean annual increment of stand volume.

Stand ID	Elevation (m)	Aspect (Slope)	Density (trees ha^{-1})	Basal area ($m^2 ha^{-1}$)	D range (cm)	Mean Height (m)	MAI ($m^3 ha^{-1} a^{-1}$)
29β	1030	N-NE (20%)	747	25.28	10-32	23	5.981
59β	1310	N (22%)	783	17.02	10-32	14	4.172
24β	1513	NE (32%)	1003	21.70	10-36	17.43	7.522
14a	1820	N (42%)	697	20.42	10-60	13.85	2.675

The following variables related to tree dimensions were recorded for each sample tree: diameter at 0.30 m above ground (D_B), diameter at 1.30 m *(D)*, diameter at the base of the live crown (D_C), the total height *(H)*, the height to the base of the live crown (H_S), and diameters (D_{BR}), lengths (L_{BR}) and height above ground for all the branches. The tree bole was cut at 0.30 m and at 1 m intervals thereafter up to the base of the live crown (*i.e.*, the point where the main stem bifurcated), and the part of the stem within the crown was separated from the branches. After felling the tree, the stump (*i.e.*, the segment of the stem from ground to 0.30 m above ground) was also removed. The leaves on each branch were collected and put into plastic bags. The stem sections (including bark), the stump, the branches and the leaves (*i.e.*, the whole tree excluding roots) were transported to the laboratory and oven dried to constant weight at 80 °C. The dry mass of each component was subsequently weighted. Before felling, the horizontal extension of the eight longest branches (excluding epicormics) were projected down onto the ground and the horizontal crown projection area (P_R) was determined assuming that it could be compared to a circle or to an ellipse.

Stefanidis (2001) measured diameter distribution within the beech stands and the equations developed from the 16 trees were subsequently applied to these distributions so as to obtain estimates of biomass for stem, branch and foliage components at the stand scale. Procedures that estimate bias in the developed allometric relationships are reported in the following Section.

4.2.3 Regression analysis

Foresters and ecologists have used different models for estimating forest biomass. Undoubtedly, the most commonly used mathematical model is the allometric equation with the following power form:

$$Y = aX^b \qquad \text{Eq. (4.1)}$$

where a and b are scaling parameters that vary with the variables under investigation; Y is the total biomass or one of its components and X a tree dimension variable (*i.e.* D, D^2, D^2H, DH, *etc*).

Payandeh (1981) further classified model (Eq. 4.1) into two types: the "intrinsically linear" type which assumes a multiplicative error in the raw data and the "intrinsically nonlinear" type with an additive random error. In the "intrinsically linear" model, the original data are log-transformed and the ordinary least square method is used to estimate the parameters. In many cases, log-transformation of raw data results in homoscedasticity of the dependent variable Y, a prerequisite for regression methods. However, even though the logarithmic equation is mathematically equivalent to Eq. (4.1), it is not identical in a statistical sense (Zar, 1968). Using the logarithmic form of equation (4.1), produces a systematic underestimation of the dependent variable Y when converting the estimated $\ln Y$ back to the original untransformed scale Y. Although this inherent bias has long been recognised (Finney, 1941), concern for its potential impact on estimates of biomass is relatively recent (Madgwick, 1970; Mountford and Bunce, 1973; Sprugel, 1983). Several procedures for correcting bias in logarithmic regression estimates have been advocated (Baskerville, 1972; Beauchamp and Olson, 1973; Yandle and Wiant, 1981; Sprugel, 1983).

Let $\hat{Y} = e^{\ln\hat{a} + \hat{b}\ln X}$ be the mean predicted value for a given X in arithmetic units. According to Baskerville (1972), an approximation of the corrected, unbiased estimate is

$$\hat{Y}_c = e^{\ln\hat{a}+\hat{b}\ln X+Q}$$

where $Q = SEE^2/2$ is the correction factor (CF) and $SEE = \sqrt{\sum(\ln Y_i - \ln\hat{Y}_i)^2/(n-p)}$ is the standard error of the estimate of the regression; n and p denote the number of the observations and the fitted parameters, respectively.

Madgwick and Satoo (1975), found from *simulated* intensive sampling of actual tree mass that with some corrections, values tended to be overestimated. They suggested, that as the bias from re-transformation is generally small compared to the overall variation in the estimate of biomass, the correction factor be ignored. In addition, Beauchamp and Olson (1973), reported that data on stem biomass of *Liriodendron tulipifera* L. showed small bias (< 1%) in the predicted dry mass obtained from the biased (uncorrected) estimate. For the purposes of the present study, a and b values are reported for the biased regression, in conjunction with the correction factor CF as given by Sprugel (1983).

Yandle and Wiant (1981) reported that the bias

$B = \hat{Y}_c - \hat{Y}$, as a percent of the unbiased estimate is

$$B_P = ((e^Q-1)/e^Q)100 \qquad \text{Eq. (4.2)}$$

and is constant over the range of X values (B_P is the percent bias and Q is the correction factor).

Wiant and Harner (1979) suggested that it is informative to express the standard error of $\hat{Y}_c$ for a given X as a percent of $\hat{Y}_c$. Thus

$$G = (e^{Q}-1)^{1/2}100 \qquad \text{Eq. (4.3)}$$

which is also constant over the range X values (G denotes the percent standard error). Usually, the validity of the relationship is tested by the coefficient of determination of the logarithmic regression, R^2, and SEE is computed for the entire dataset of the transformed data. However, high values of R^2 and small values of SEE (typically obtained in allometric studies) do not guarantee precision of the estimate, when values are back transformed to the linear scale. Thus, it is not unusual that, for a particular tree diameter, the predicted biomass $\hat{y}$ deviates by a relative amount of 90% from the corresponding observed value.

On the other hand, the general linear regression procedure does not apply to the "intrinsically nonlinear" model and iterative procedures are required for estimating the allometric parameters. Payandeh (1981) reviewed and compared the log-transformed linear model with the simple nonlinear form and found that the latter model resulted in better fit for two datasets of *Betula alleghaniensis* Britton and *Acer saccharum* Marsh. Nonlinear models for total aboveground, stem, branch and foliage biomass were based on the 16 sample trees and developed with appropriate routines in SPSS software.

It is common in allometric studies that the relationships obtained rarely validated with data other than the data that were used in the regression analysis. Madgwick (1970) pointed out that if the models are to be used for prediction purposes, they

should be evaluated with independent data. Moreover, it must be emphasised that allometric relationships are only valid over the range of the independent variable X, and extrapolation to either higher or lower values of X may result in large deviations between real and predicted values. However not many data have been collected in order to test thoroughly the errors arising from these causes.

Parresol (1999), reported several statistics for evaluating goodness-of-fit and for comparing alterative biomass models. The mean percentage difference (MPD) between the predictions and raw data was used to assess the performance of different models. This statistic gives the average deviation of the regression, relative to the raw data, and assesses the variability of the fitted equation. MPD is calculated as the average of differences between observed and predicted values divided by the observed (Payandeh, 1981; Niklas, 1994).

A desirable feature of tree component regression equations is that mathematical functions developed for different tree compartments should be consistent with each other, and in terms of the additivity property (Kozak, 1970). That is, if one tree component is part of another component, the estimate of the part should not exceed the estimate of the whole. In addition, the sum of the sub-components should equal - in statistical terms – the regressed estimate of the total (Chiyenda and Kozak, 1984). Recently, Parresol (2001) developed two procedures to force additivity on a set of nonlinear tree biomass functions. In the first method, the total biomass regression is defined as the sum of the separately calculated best-fit regressions of the components. The second procedure is more difficult to employ and nonlinear seemingly unrelated regressions are used (Parresol, 2001). In other words, the error inherent in the sampling protocol is not assumed to be constant for the harvested trees, but is modelled using appropriate techniques. Additivity problems arise mainly from the stratified procedures used to estimate tree biomass. However, in this Chapter, the biomass data were collected after complete harvest of the trees, and only small errors are, therefore, expected from the additivity property.

4.3 RESULTS

4.3.1 Allometric equations

Scatter plots of the data indicated that biomass values for different tree components, as well as values for H, H_S, D_C and P_R, were non-linearly related to D. Subsequently, the raw values were transformed using the Napierian logarithmic function and the least squares method was applied to estimate the parameters of the developed models. The results are presented in Table 4.2a and surprisingly strong relationships were obtained in almost all cases.

Table 4.2a: Regression equations of the form $Y = \ln a + bX$. The parametric values are significantly different from zero at the 5%-level. The coefficient of determination R^2, and the standard error of the estimate for 14 degrees of freedom SEE, were calculated in arithmetic units. The number of sampled trees is 16.

Y	X	ln$a$	b	R^2	s.e (a)	s.e (b)	SEE
ln$M$	ln$D$	-1.3816	2.3485	0.99	0.2080	0.0724	0.1841
lnM_S	ln$D$	-1.6015	2.3427	0.98	0.2358	0.0821	0.2088
lnM_{BT}	ln$D$	-5.2898	2.9353	0.97	0.3686	0.1284	0.3264
lnM_{BC}	ln$D$	-6.3807	3.1037	0.95	0.5573	0.1941	0.4936
lnM_{BE}	ln$D$	-5.9523	2.7501	0.76	1.2032	0.4191	1.0657
lnM_{FT}	ln$D$	-4.1814	1.6645	0.90	0.4362	0.1519	0.3863
lnM_{FC}	ln$D$	-5.5168	1.9979	0.87	0.5970	0.2079	0.5287
lnM_{FE}	ln$D$	-3.5789	0.9021	0.40	0.8420	0.2933	0.7458
lnM_{SP}	ln$D$	-1.7716	1.0730	0.78	0.4398	0.1532	0.3895
lnM_{CS}	ln$D$	-4.0543	2.2116	0.87	0.6683	0.2328	0.5918
lnM_{CW}	ln$D$	-4.1293	2.6741	0.97	0.4038	0.1407	0.3576
ln$H$	ln$D$	1.4192	0.5358	0.89	0.1459	0.0508	0.1292
lnH_S	ln$D$	1.2238	0.4677	0.75	0.2052	0.0715	0.1818
lnD_C	D	1.1544	0.0504	0.91	0.0949	0.0042	0.1869

M: total aboveground biomass, M_S: stem mass, M_{BT}: branch mass (including epicormic), M_{BC}: branch mass in crown, M_{BE}: mass of epicormic branches, M_{FC}: foliage mass in crown, M_{FE}: foliage mass of epicormics branches, $M_{FT} = M_{FC} + M_{FE}$, M_{SP}: stump mass, M_{CS}: the mass of the stem within the crown, $M_{CW} = M_{BC}+M_{CS}$. For D, D_C, and H see Section 4.2.2. The biomass is expressed in kg, the diameters in cm, and height in m.

In one case however, the mass of the leaves of the epicormics branches (M_{FE}) was not highly correlated to D as indicated by the R^2 of the log-transformed data. The

MPD for M_{BE} was about 87% (Table 4.2b) but D explained 76% of the variability of the biomass of epicormic branches. Stronger relationships are reported for total foliage biomass (M_{FT}) and for the mass of leaves found in the canopy (M_{FC}). In the following equations, H is introduced as the second independent variable and slightly better predictions for M_{FT} and M_{FC} were obtained than with the allometric equation including only D:

$M_{FT} = 0.0001997(0.000012)D^2H + 0.331(0.227), \quad R^2 = 0.9493$ Eq. (4.4)

and

$M_{FC} = 0.0001663(0.000013)\ D^2H + 0.224(0.243), \quad R^2 = 0.919$ Eq. (4.5).

The standard errors of the estimates are presented in the parentheses; in both equations the slopes were statistically different from zero but the 95% range of the intercepts included this value. However, the addition of H for predicting the biomass of other tree components did not substantially contribute to an increase of R^2 or to decrease of SEE. The height of the stem was also closely related to D according to $H_S = 3.4001D^{0.4677}$ (as transformed from the logarithmic equation in Table 4.2a).

Stump mass generally increased with increasing D (see Table 4.2a) or D_B (Figure 4.1) but a large variability occurred, which resulted in a rather low R^2. Subsequently, the stump shape was approximated as a cylinder with diameter and height equal to D_B and 0.3 m respectively, and the standard volume formula was used for predicting M_{SP}; however, this approach did not significantly decrease the SEE (data not shown).

A highly significant exponential relationship between $\ln D_C$ and D was obtained (Table 4.2a) which, after transformation of the coefficients to arithmetic scale reads as

$$D_C = 3.172e^{0.0504D} \quad \text{Eq. (4.6)}$$

where e is the base of Napierian logarithms.

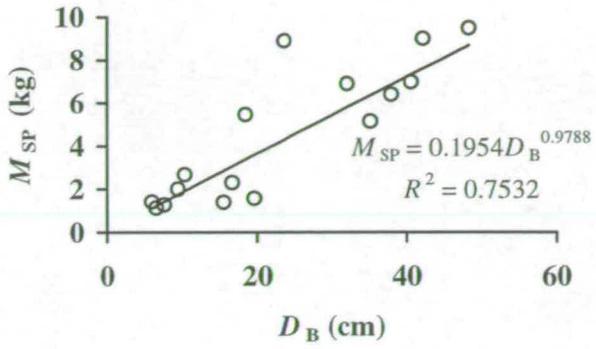

Figure 4.1: Stump biomass M_{SP} in relation to diameter at 0.30 m aboveground D_B. The slope is statistically different from one.

The horizontal projection area of crown (P_R), was also non-linearly related to D and the empirical relationship was

$$\ln P_R = 1.2830(0.1121)\ln D - 0.9004(0.321) \qquad \text{Eq. (4.7a)}$$

with $R^2 = 0.9034$, and standard errors in parentheses.

The percent bias was computed according to Eq. (4.2) and resulted in a rather low estimate of 3.98% (see Table 4.2b). Thus, no procedures were adopted in order to eliminate the inherent bias and the antilogs of the logarithmic predicted values were used to derive the power function

$$P_R = 0.4064 D^{1.2830} \qquad \text{Eq. (4.7b)}$$

with sum of squared errors, SSE = 1021.99 (on the linear scale); the projection area was measured in m^2 and D in cm. Larger values of percent bias (43.43%) were obtained for the equation that relates the biomass of epicormics branches (M_{BE}) to D; however, the SSE of the biased and corrected equations was 12,658 and 12,657 respectively (in linear scale), indicating that unbiased predictions do not significantly reduce the residual error. Finally, the pooled data for the branches were used to derive the following relationship between branch biomass M_{BR} and branch diameter D_{BR}:

$$\ln M_{BR} = 3.415\ (0.062) + 2.818\ (0.056)\ \ln D_{BR} \qquad \text{Eq. (4.8)}$$

with $R^2 = 0.889$, SEE = 0.6871, and standard errors of parameters in parentheses.

Table 4.2b: Statistical values for the standard error of the estimate (SEE) for 14 degrees of freedom, the correction factor (CF), and the sum of square for error (SSE) calculated in arithmetic units, respectively. Percent bias and Percent s.e were computed with Eq. (4.2) and Eq. (4.3) respectively. The statistical parameters are referred to the equations presented in Table 4.2a.

Y	X	SEE	CF	Percent bias	Percent s.e	SSE	MPD (%)
$\ln M$	$\ln D$	0.18	1.01	1.68	18.57	139617.36	14.00
$\ln M_S$	$\ln D$	0.20	1.02	2.15	21.10	91511.54	16.06
$\ln M_{BT}$	$\ln D$	0.32	1.05	5.19	33.53	14925.35	25.38
$\ln M_{BC}$	$\ln D$	0.49	1.12	11.47	52.52	13605.48	37.82
$\ln M_{BE}$	$\ln D$	1.06	1.76	43.32	145.38	12658.01	86.89
$\ln M_{FT}$	$\ln D$	0.38	1.07	7.19	40.11	10.94	39.92
$\ln M_{FC}$	$\ln D$	0.52	1.15	13.04	56.79	8.67	40.26
$\ln M_{FE}$	$\ln D$	0.74	1.32	24.27	86.26	3.25	59.36
$\ln M_{SP}$	$\ln D$	0.38	1.07	7.30	40.48	35.3	27.86
$\ln M_{CS}$	$\ln D$	0.59	1.19	16.02	64.77	1328.3	44.47
$\ln M_{CW}$	$\ln D$	0.35	1.06	6.19	36.93	12433.56	34.60
$\ln H$	$\ln D$	0.12	1.00	0.83	12.97	112.13	9.50
$\ln H_S$	$\ln D$	0.18	1.01	1.63	18.33	86.75	14.12
$\ln D_C$	D	0.18	1.01	1.73	18.86	121.69	14.37
$\ln P_R$	$\ln D$	0.28	1.01	3.98	29.09	1021.99	37.27

Moreover, the lengths of the branches were regressed on their diameter and the fitted equation is illustrated in Figure 4.2. The fitted regression was obtained through the least squares method (after log-transformation of the raw values) and the standard error of the scaling exponent was 0.0185.

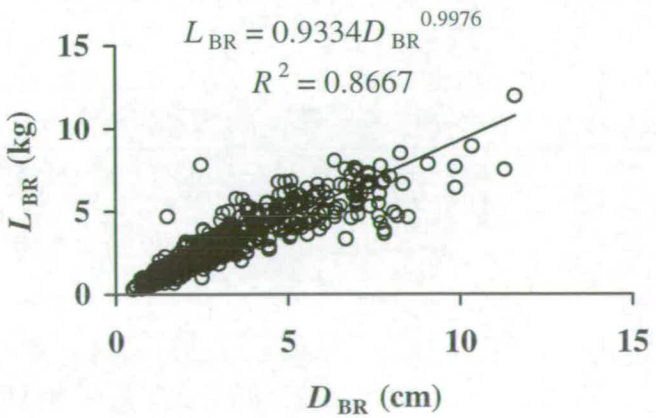

Figure 4.2: The regression of branch length L_{BR} against branch diameter D_{BR}.

To test whether the property of additivity holds for the developed total aboveground biomass equations, the separate predictions obtained from the stem, branch, and foliage regressions (see Table 4.2) were aggregated estimate *M*. The results were compared to the *M* predictions obtained from the total aboveground regression. Eight diameter classes that cover the range of the harvested trees were used to estimate biomass for the major aboveground tree parts. In Table 4.3, the values of the diameter classes and the corresponding biomass estimates are presented. In the last column the percentage difference between sum predictions and estimates from the total aboveground regression are reported.

Table 4.3: Total aboveground biomass as modelled by the regressed equation and from the summation of the predictions obtained for different tree components. In the last column the percentage difference is also presented (PD).

D (cm)	*M* (kg)	M_S (kg)	M_{BT} (kg)	M_{FT} (kg)	SUM (kg)	PD (%)
5	10.99	8.74	0.56	0.22	9.53	-13
10	56.02	44.38	4.3	0.70	49.39	-11
15	145.17	114.74	14.16	1.38	130.28	-10
20	285.3	225.11	32.95	2.23	260.30	-8
25	481.85	379.7	63.43	3.24	446.38	-7
30	739.37	582.02	108.33	4.39	694.75	-6
35	1061.9	835.17	170.32	5.67	1011.17	-4
40	1453.06	1141.9	252.05	7.08	1401.06	-3

The mean percentage difference for the eight diameters is less than -8%. This indicates that the additivity problem does not strongly influence estimation of the total biomass in the studied forest. The larger values of the PD estimate occur for small trees (< 15 cm), while for big trees, the PD is less than -8%.

The equations developed so far were assumed to comply with the 'intrinsically linear' model and the least squares method was applied to log-transformed data in

order to derive empirical values for the parameters of the allometric relationships. However, if one assumes an additive error term in the original data, then predictions should be based on 'intrinsically nonlinear' models. The underlying model requires iterative procedures (Payandeh, 1982) for parameter estimation. Nonlinear equations were developed for the major tree biomass compartments (Table 4.4).

Table 4.4: Regression equations of the form $Y = aX^b$. Symbols as in Table 4.2.

Y	X	a	b	R^2	s.e (a)	s.e (b)	SSE	MPD (%)
M	D	0.9402	1.9643	0.97	0.4897	0.1474	87058.6	25.77
M_S	D	0.7568	1.9536	0.97	0.4007	0.1498	54623.8	25.88
M_{BT}	D	0.1097	2.0545	0.91	0.116	0.2985	8467.7	45.43
M_{FT}	D	0.0057	1.9836	0.96	0.0035	0.1758	5.23	39.92

Finally, the data obtained from the sixteen sampled beech trees were used in order to validate the performance of the SSS that was presented in Section 3.3.2. According to this method, the trees with the smallest diameter in the dataset were used to select two equations from the meta-database (see Table A1). In Figure 4.3, the regressions developed from the sixteen trees and the SSS method are depicted. The MPD for the empirical regression (which was based on the sixteen harvested trees) and the SSS equation (which was based on the two smallest trees) is 14 and 24 %, respectively.

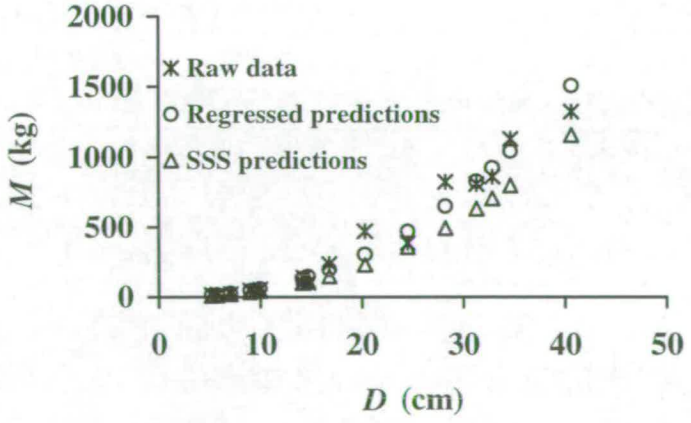

Figure 4.3: Predictions of total aboveground biomass for beech trees from the empirical regression and the SSS method. Raw data are also depicted.

4.3.2 Estimation of stand biomass

The dry biomass (Mg ha^{-1}) of different tree components for the 23 studied stands is presented in Table 4.5. The average aboveground biomass (S_T) amounted to 192.49 Mg ha^{-1}, with the maximum value (229.48 Mg ha^{-1}) obtained at 1210 m, and the

Table 4.5: Estimated biomass for the beech stands in Vermio mountain (Naousa forest). The allometric equations presented in Table 4.2a were applied to the *D* distributions of the stands to derive the biomass values.

Stand ID	Elevation (m)	Aspect (Slope)	Density (trees ha^{-1})	Basal area (m^2 ha^{-1})	Stem (Mg ha^{-1})	Branch (Mg ha^{-1})	Foliage (Mg ha^{-1})
29β	1090	N-NE (18%)	747	25.28	186.71	29.42	1.75
20	1210	N (22%)	577	22.66	131.12	20.05	1.27
35	950	N (31%)	767	24.02	173.87	27.38	1.64
34α	1200	N (25%)	930	23.84	170.26	25.19	1.72
59β	1300	N (22%)	783	17.02	118.62	17.02	1.25
19α	1300	N (24%)	877	22.22	168.98	25.84	1.59
18	1200	E (10%)	673	24.25	184.88	30.56	1.65
36	1320	E (15%)	1130	23.37	191.53	28.45	1.95
7	1300	NE (55%)	860	25.25	184.18	28.27	1.78
17β	1400	N (16%)	720	23.05	171.31	27.27	1.59
46	1300	N (20%)	913	24.89	179.26	27.08	1.75
16β	1500	N (30%)	667	20.10	147.86	22.98	1.41
24β	1520	NE (32%)	1003	21.70	154.02	25.03	1.39
9γ	1620	NE (46%)	620	22.71	172.32	28.34	1.54
26β	1360	W (29%)	977	21.99	154.87	22.44	1.61
56β	1510	N (25%)	1230	15.56	96.99	11.23	1.28
15β	1730	E (28%)	613	20.21	152.87	24.98	1.39
23	1470	N (22%0	990	25.21	179.93	27.35	1.79
14β	1680	E (35%)	713	21.80	160.12	25.01	1.52
48	1700	N (40%)	670	24.65	192.43	33.24	1.66
8α	1400	N (55%)	670	21.96	182.1	28.29	1.77
5	1210	N (45%)	830	26.78	197.04	30.56	1.87
14α	1960	N (42%)	697	20.42	149.7	23.39	1.43

minimum (109.51 Mg ha^{-1}) at 1510 m. Stem (S_S), branch (S_B) and foliage biomass (S_F) averaged 165.26, 25.63 and 1.59 Mg ha^{-1}, respectively. A short review of several biomass studies for beech stands conducted throughout Europe is presented in Table 4.6.

Table 4.6: Published biomass data of above ground tree compartments from European beech forests.

Stem Mg ha^{-1}	Branch Mg ha^{-1}	Foliage Mg ha^{-1}	Total Mg ha^{-1}	Country	Reference
318	50.8	3	371	Belgium	Duvigneaud and Kastemont (1975)
213.6	22.4	2.9	248.9	Belgium	Duvigneaud and Kastemont (1975)
169.6	24.2	3.8	197.6	Bulgaria	Garelkov (1973)
280	31.6	2.9	314.5	Bulgaria	Garelkov (1973)
364.7	49.1	4.7	418.5	Bulgaria	Garelkov (1973)
124	N/A	2.5	126.5	Denmark	Moller *et al.* (1954)
72.35	11.35	2.8	86.5	France	Ottorini and Le Goff (1998)
287	29	2.7	318.7	Italy	Calamini *et al.* (1983)
144.82	30.33	N/A	175.15	Italy	Visona *et al.* (1975)
100.7	29.4	2.7	134.6	Spain	Santa Regina *et al.* (1997)
9.96	0.64	3.01	13.61	Holland	Bartelink (1997)
4.37	0.29	1.28	5.94	Holland	Bartelink (1997)
63.1	8.45	3.61	75.16	Holland	Bartelink (1997)
63.91	9.54	3.08	76.52	Holland	Bartelink (1997)
126.9	33.38	4.22	164.5	Holland	Bartelink (1997)
123.3	39.49	3.93	166.72	Holland	Bartelink (1997)

Santa Regina *et al.* (1997) did a similar study in northern Spain and they reported a value of 134.6 Mg ha^{-1} for total biomass in a *Fagus sylvatica* forest with a density of 523 trees ha^{-1}. Visona *et al.* (1975) investigated the aboveground biomass in a coppice beech forest in Central Italy at 1709 m altitude and estimates a value of 144 Mg ha^{-1} for total aboveground biomass. The maximum value of aboveground biomass was 418.5 Mg ha^{-1} reported by Garelkov (1973) in Bulgaria and the minimum (5.94 Mg ha^{-1}) was obtained in Holland (Bartelink, 1997) for an 11-year

old stand. The biomass estimations from the 23 studied stands all fall within this range.

A regression analysis made to investigate the relationship between standing biomass and altitude did not reveal any significant trend (R^2= 0.006) for the Greek forest. However, the ratio of the biomass on a per hectare basis present at the highest elevation stand to the biomass of the lowest elevation stand was 0.86 for total aboveground, 0.86 for stem, 0.85 for branch and 0.87 for foliage biomass. An increase of about 900 m in absolute altitude resulted in *ca* 16% difference in total standing biomass. A similar degree of variation was reported by Satoo (1977) for beech stands in Japan. Garelkov (1973) estimated the aboveground biomass in Bulgaria and a 45% difference was observed between sites with different productivity potential.

The stand foliage biomass (S_F) estimated for the studied forest ranged from 1.25 to 1.95 Mg ha^{-1} and is below the values reported in several European studies (see Table 4.6). Tatsuhara and Kurashige (2001) estimated the foliage biomass of a *Fagus crenata* (Blume) forest in central Japan across an elevation gradient stretching from 390 to 1180 m above sea level and S_F ranged from 2.20 to 4.22 Mg ha^{-1} in accordance to the European values. However, the same sampling and statistical procedures were not followed in the studies cited above and thus interpretation of different S_F values at the global scale should be considered tentative.

The total aboveground biomass was very strongly linearly related to stem biomass (R^2= 0.99, P<0.001) while the ratio of the two variables (S_T/S_S), averaged 1.16 (Figure 4.4A). The regression line takes the following form:

$$S_S = 0.837\ S_T + 4.1238 \qquad \text{Eq. (4.9)}$$

Very strong linear relationships were also obtained when branch and leaf stand biomass were plotted against stem biomass (Figure 4.4B and C). Finally, leaf stand

biomass was also regressed against branch biomass and the formulated model gave an R^2= 0.46 with $P < 0.001$ (Figure 4.4D). It should be kept in mind that for all regressions reported in Figure 4.4, the smallest D size of the recorded trees is 10 cm and thus, the interpretation of these empirical models should be applied only for the given range of the biomass values. Extrapolation beyond these values could result in very high deviations between real and predicted estimations.

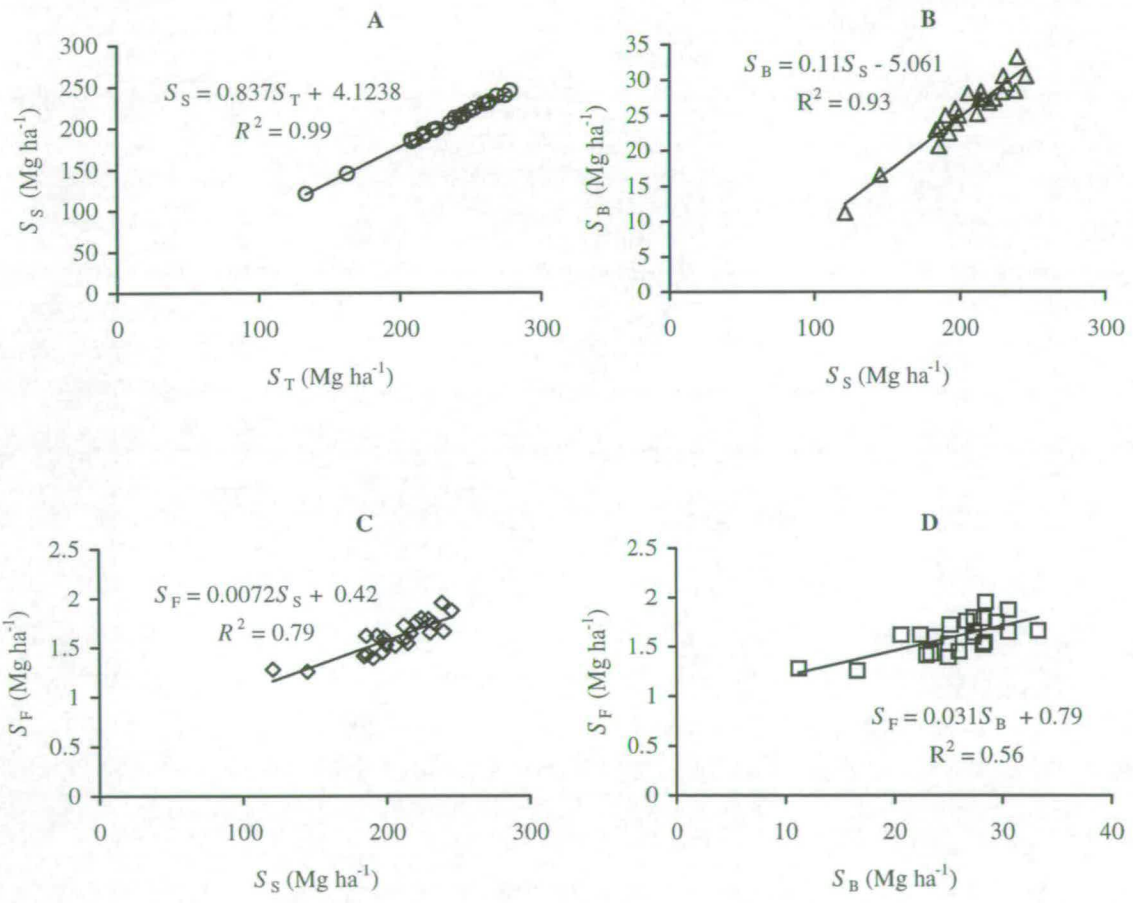

Figure 4.4: Regression of **A**) stem stand biomass to total aboveground stand biomass, **B**) branch stand biomass against stem stand biomass, **C**) foliage stand biomass against stem stand biomass and **D**) leaf stand biomass against branch stand biomass.

4.4 DISCUSSION

4.4.1 Allometric regressions

Diameter at breast height explained much of the variability in biomass values of different tree components. Adding H as a second variable improved predictions for foliage biomass in accordance with Bartelink (1997). However, tree height did not substantially decrease the SEE for the regressions of total, stem, and branch biomass. The high correlation between D and H may explain the low gains in predictions when the latter variable is included in allometric models (multicollinearity).

Strong scaling relationships were also found between different tree dimensions (*e.g.*, P_R, D_C, H_S) and D as well as between branch biomass and branch diameter. It is clear that stump biomass is not so tightly related to either D or D_B as indicated by the R^2 values (Table 4.2a and Figure 4.1). An explanation could be that the sample trees were located on sites with different slopes, which in turn may influence the shape – *e.g.*, presence of buttresses – of the lowest part of the stem. This variability in shape could not be captured by D_B alone and it is possible that other variables might be more useful in predicting stump biomass. However, the information collected from the harvested trees could not be used to test thoroughly this hypothesis and compared to total tree biomass, stump mass is a very small proportion and any deviations from real values would be insignificant when extrapolated to stand scale.

In statistical terms, the highest inherent bias recorded in the dependent variables after log-transformation was for the biomass of epicormic branches: the percentage bias value was 43.32% (Table 4.2b). Applying the appropriate formula to eliminate this bias, the SSE was insignificantly reduced (from 12658.01 to 12657.9). This observation was also true for other tree components, in agreement with Beauchamp and Olson (1973) and Madgwick (1970). When nonlinear models (Table 4.4) were compared with log-transformed regressions (Table 4.2a and Table 4.2b) it appeared that the former fitted the field data better than the latter as implied by the SSE. However, in terms of MPD, the intrinsically linear models appeared to deviate less

than the simple power functions for total aboveground, stem and branch biomass. This outcome is in disagreement with the results presented by Payandeh (1981), who concluded that 'intrinsically nonlinear' models gave better estimations than the log-transformed equations. In addition, the values of the correction factor were very small for all the equations developed (Table 4.2b), implying that the inherent bias in the 'intrinsically linear' models does not really affect the predictions made by these regressions.

Values of MPD for crown components (foliage and/or branches) were generally large (Table 4.2b) and this indicates that incorporating a second variable could decrease the deviation between observed data and predicted values. However, one should be very careful about which variables to use, so as to avoid statistically confounding the results. For example, adding any variable that is related to the linear dimension of trees (in conjunction with D), would result in the phenomenon termed collinearity or multicollinearity of the regression. This statistical pitfall arises because the regressor variables are highly related to each other (Sokal and Rohlf, 1995). In turn the coefficient of determination decreases while MPD reaches a larger value. Theoretical models (Shinozaki *et al.*, 1964), and empirical information (Bartelink, 1997), suggest that sapwood area at breast height explains more of the variability in crown biomass than D alone. However, such data were not available for the sampled trees so that further analysis could not take place.

As is reported in Table 4.3, the property of 'non-additivity' in developed biomass regressions, influences the smaller trees by 12% more than the larger trees. Thus, it can be supported that at the stand level (where the diameter of most individuals is more than 15 cm), quite accurate estimations are expected if one applies either the aggregation procedure or the regression equation formulated for the total aboveground biomass.

Fairly good total aboveground biomass predictions were obtained by the SSS method, which was presented in Chapter 3. The MPD value is 24% (see also Figure

4.3), while Pastor *et al.*, 1983/1984 reported that original regressions (*i.e.*, regressions based on several harvested trees) may yield a value of MPD up to 30%. This outcome is in accordance with the results reported for the ten compiled studies (Table 3.9).

Since data were pooled from stands with different structural and topographical characteristics (Table 4.1), one could expect that quite accurate estimates may be obtained if the equations presented are applied throughout the study forest. Thus, the relationships established may be quite useful for the sustainable management of the forest, since no model existed previously for biomass estimations.

4.4.2 Biomechanical analysis

Apart from the practical usefulness of the formulated relationships, inferences about the physical forces acting upon the sampled trees can be made by comparing empirical values of the allometric exponents to the theoretical ones. The three different theoretical models that describe the biomechanical properties of trees, have been presented in Section 2.2.3 (see also Table 2.3).

McMahon and Kronauer (1976) examined the scaling of tree height based on stress and elastic similarity models and Niklas (1994) reported that, for very old dicot trees, $H \propto D^{0.474}$ implying that mature trees taper so as to maintain a constant elasticity throughout the tree. In this study, the 95% confidence intervals for the reduced major axis scaling exponent of H against D are 0.45-0.66 and indicate that wind-pressure dynamic loadings most likely affect the size-shape relationship of the study trees (see Section 2.2.3).

The reduced major axis value for the scaling exponent in L_{BR}-D_{BR} relationship is 1.0715, and the 95% confidence intervals are 1.0318-1.1112, indicating that branch length increases almost exactly in direct proportion to branch diameter, and still resists elastic buckling (see also Table 2.3). Thus the null hypothesis (geometric similitude, *i.e.*, $L_{BR} \propto D_{BR}^{1}$) is not rejected, whereas the stress and elastic similarity

models, appear inappropriate to describe the allometry of branch length in relation to branch diameter (Figure 4.2). Different conclusions were reached by Bertram (1989), who reported that branches collected from a silver maple tree (*Acer saccharinum*, measuring 13.2 m in height) conformed to the elastic similarity model, whereas the length of the peripheral twigs scaled to the diameter according to the geometric model (*i.e.*, the exponent was not statistically different from one).

Niklas (1994) supported that the three classical biomechanical models do not take into account the effects of stem ontogeny on the functional relation between stem length and diameter. He proposed that young trees can grow under the isometric relation of H against D, without collapsing under their own weight. As trees age and accumulate wood in their secondary growth layers , the elastic similarity model should better describe the H-D relation, while with extreme age and size, the scaling of height may shift to rebound stress induced forces. However, the data collected from the study forest are not adequate to test these hypothesis.

At the stand level, foliage biomass was positively related to stem biomass (Figure 4.4C), suggesting that relatively more foliage was allocated to stands which produce more stem wood on a per hectare basis. The close correlation between branch and stem biomass (Figure 4.4B), may be explained on a biomechanical basis. More stem wood is needed to support large amount of branches so as to sustain pressures induced by static and dynamics forces. Finally, estimation of belowground biomass (coarse and fine roots) did not take place since appropriate models could not be developed for the studied forest.

5. ABOVEGROUND NET PRIMARY PRODUCTIVITY OF A BEECH (*Fagus moesiaca* Cz.) FOREST: THE CASE STUDY OF NAOUSA FOREST, NORTHERN GREECE

5.1 INTRODUCTION

Biomass, net primary productivity (NPP), and leaf area are key characteristics of autotrophic ecosystems since they help define the standing crop, the fluxes of carbon and nutrients, and set upper limits on water use through transpiration and on carbon fixation through photosynthesis (Gholz, 1982). Forests - the most extensive terrestrial ecosystems - cover approximately 30-40% of the Earth's ice-free land surface and play a significant role in important biospheric processes (Waring and Running, 1998). Additionally, forested ecosystems are currently hypothesised to provide a major CO_2 sink that helps stabilise the global carbon balance (Tans *et al.*, 1990).

Fassnacht and Gower (1997) advocate that a better understanding of the factors controlling forest production is needed to increase the reliability of estimates of the role of forests in the global carbon dynamics. Moreover, in the era of the ecologically sound management of forest ecosystems, net primary production should be estimated if a holistic approach to stand dynamics is to be achieved. Net primary productivity (NPP) of natural ecosystems is defined as the increase of plant biomass per unit area and unit time, having also accounted for literfall production (Kimmins, 1997). It is well documented that, apart from effects caused by genetic differences among species or ecotypes, characteristics of a site can strongly affect production and growth of plant biomass (Kaufmann and Ryan, 1986; Lindenmayer *et al.*, 1999).

Foresters and ecologists have focused their attention on understanding the changes in the physical and chemical characteristics of ecosystems in relation to different site

factors and how these influence the growth of plants (Nihlgard, 1972; Kimmins, 1977; Erricsson, 1994; Laskowski, *et al.*, 1995; Schmidt and Carmean, 1998; to name but a few). Many efforts to relate foliar chemical concentrations, growth and site productivity (Radwan and Harrington, 1986; Harrington *et al.*, 1995) and leaf area to nutrition availability (Vose and Allen, 1988) have been reported. More recently carbon isotope discrimination in tree organic matter has also been used as an indicator of growth and related to water availability (*e.g.*, McNulty and Swank, 1995) and other environmental variables (*e.g.*, O'Leary, 1981; Farquhar *et al.*, 1989).

In addition, aboveground net primary productivity (ANPP), growth efficiency (determined as net primary production per unit leaf area) and leaf area are common related measures of forest site productivity and structure. The interrelationships between leaf area index (L^*) and productivity have not been widely investigated in broadleaved stands - however, see Bolstad *et al.* (2001) - while a theoretical approach to explain the NPP- L^* relationship was presented by Jarvis and Leverenz (1983). It is generally agreed that progress in understanding ANPP and its controls in forest ecosystems is hindered by the limited existing field data (Clark *et al.*, 2001, Gower *et al.*, 2001). Net primary production of forests, also defined as gross primary production (GPP) minus autotrophic respiration, is a key descriptor of the carbon cycle of forest ecosystems (Li *et al.*, 2002) and according to the IGBP (Terrestrial Carbon Working Group, 1998) the estimation of NPP at the forest scale is fundamental to the prediction of regional and global net ecosystem and biome production.

It is unquestionable that researchers throughout Europe have produced a voluminous amount of work directed towards understanding the ecological processes that govern natural ecosystems. Nevertheless, this is not the case for Greek forest ecosystems. The knowledge obtained so far for woody biomass production of forests in Greece in relation to abiotic variables is limited. European beech (*Fagus sylvatica* L.) is the major broadleaved tree species in central and western Europe but also extends further south in the Mediterranean basin, where it is confined to mountainous regions

(Garcia *et al.*, 2000). In Greece, beech (*Fagus moesiaca* Cz.) forests occupy 337,000 ha (Gatzojiannis, 1996), *ca* 13.41% of the total Greek forested surface with mean annual increment of 4.7 m^3 ha^{-1} a^{-1} (FRI, 1986). Economically, it is considered the most productive broadleaf, in addition to oaks (*Quercus* spp.) and chestnut (*Castanea sativa* Mill.). However, not much original information is available to define the physiological responses of this species to different environmental variables.

In this Chapter a preliminary study on the aboveground net primary productivity of a beech forest (*Fagus moesiaca* Cz.) in northern Greece is presented. The following three objectives were set:

(i) to determine the ANPP, L^* and the growth efficiency of the beech stands,
(ii) to test whether ANPP, L^*, and growth efficiency varied with elevation and
(iii) to determine whether trees growing at higher elevation may be under environmental stress and to relate to the different values of ANPP, L^*, and growth efficiency to this stress.

5.2 MATERIALS AND METHODS

5.2.1 Study area

The forest studied (40°32N, 21°58E) is located on the eastern slopes of Vermio Mountain, spanning from 380 to 2052 m above sea level and belongs to the Municipality of Naousa town. The following tree species (*Pinus nigra, Abies borissi-regis, Castanea sativa, Ilex aquifolium, Juniperus* sp., *Quercus* sp., *Salix* sp., *Populus* sp., *Platanus* sp, *Acer* sp., *Fraxinus* sp., *Buxus sempervirens, Cornus* sp., *Prunus* sp., *Rubus* sp., *etc.*) occur in this ecosystem corresponding to the range of site conditions. The climate of the forest can be classified as temperate Mediterranean with rainy winters and warm summers and according to Stefanidis (2001), the total annual rainfall is 1500 mm. Minimum rainfall occurs during the

July-August period, but atmospheric humidity is influenced by the nearby archipelagos.

Naturally regenerated, pure beech (*Fagus moesiaca* Cz.) stands occupy a total area of 2121 ha stretching from 900 m to 1970 m covering a range of different topographical characteristics (see Table 5.1). Because of the disturbed history of the forest (clearcut fellings during 19th century and several fire events during World War II), it is quite usual to encounter cohorts (within the stands) that correspond to different age and consequently tree size- classes. Selective thinnings take place according to the specific need of each stand.

5.2.2 Calculation of ANPP at stand scale

To estimate ANPP at the stand scale (the symbol for use in equations is P^S), I made use of the information provided by the forest management plans prepared in 1991 and 2001 (Stefanidis, 1991 and 2001). Twenty-three rectangular plots of 0.2 to 0.3 ha area were established in year 1991 in pure beech stands (excluding coppiced stands) covering a range of different structural and topographical characteristics. In each plot the tree diameters at breast height (D, 1.30 m above ground), the slope, the altitude and the aspect were measured; trees with D less than 10 cm were not recorded. In 2001 the 1991 plots were relocated in order to enable re-measurement of the same trees ten years later (Stefanidis, person. comm., see Table 5.1). In none of the plots were there dead or damaged trees in 2001.

The average annual P^S for the ten-year period was calculated as:

$$P^S = (\Delta B_S + \Delta B_h + 10 M_L)/10 \qquad \text{Eq. (5.1)}$$

where ΔB_S is the standing biomass increment, ΔB_h is the biomass increment of trees harvested from each stand during this period, and M_L is the average yearly production of leaf litter biomass during the 10-year period.

Table 5.1: Structural and topographical characteristics of the stands sampled in 2001. MAI stands for the mean annual increment of tree woody volume and *D* for diameter at breast height (source: Stefanidis, 1991).

Stand ID	Elevation (m)	Aspect (Slope)	Density (trees ha^{-1})	Basal area (m^2 ha)	Max. *D* (cm)	Mean Height (m)	MAI (m^3 ha^{-1} a^{-1})
29β	1090	N-NE (18%)	747	25.28	36	17.43	8.42
20	1210	N (22%)	577	22.66	34	22.31	5.98
35	950	N (31%)	767	24.02	44	23.58	10.01
34α	1200	N (25%)	930	23.84	30	17.25	6.15
59β	1300	N (22%)	783	17.02	34	17.8	8.25
19α	1300	N (24%)	877	22.22	34	24.4	9.51
18	1200	E (10%)	673	24.25	34	21.8	11.97
36	1320	E (15%)	1130	23.37	40	22.76	4.14
7	1300	NE (55%)	860	25.25	34	17.4	6.58
17β	1400	N (16%)	720	23.05	34	17.8	6.94
46	1300	N (20%)	913	24.89	32	17.6	4.61
16β	1500	N (30%)	667	20.10	32	14.3	4.17
24β	1520	NE (32%)	1003	21.70	26	16.7	8.58
9γ	1620	NE (46%)	620	22.71	34	16.9	6.70
26β	1360	W (29%)	977	21.99	54	19.98	7.04
56β	1510	N (25%)	1230	15.56	20	14.1	5.47
15β	1730	E (28%)	613	20.21	34	17.3	3.84
23	1470	N (22%0	990	25.21	42	21.7	9.62
14β	1680	E (35%)	713	21.80	34	20.3	9.70
48	1700	N (40%)	670	24.65	42	21.28	8.23
8α	1400	N (55%)	670	21.96	48	20.07	6.68
5	1210	N (45%)	830	26.78	30	21.4	10.66
14α	1960	N (42%)	697	20.42	34	18.7	4.21

To estimate the total aboveground biomass in years 1991 and 2001, the empirical parameters presented in Table 4.2a were applied to the measured diameter distributions in the allometric equation $M = aD^b$. The number of the harvested trees varied from stand to stand because of their uneven-age structure. Also the lack of sound mathematical models does not permit us to estimate accurately the wood removed during the 1991-2001 decade. However, according to Stefanidis (person. comm.), about 10% of stem volume increment was harvested from each stand during the period and this value was used for the calculation of stand productivity. However, in some stands, forest managers enforced over or under-harvesting and these adjustments were taken into account.

5.2.3 Calculation of ANPP at tree scale

Nine trees were destructively sampled in stands located at different elevations, during summer 2000 and summer 2001 (see Table 5.2). Several dendrometric variables (*i.e.*, D, H, leaf area and tree age at breast height) were measured for each sampled tree. The locations of all the branches were projected down onto the forest floor and mapped. Forty leaves were collected from each branch and frozen until further measurements. Each leaf was digitally scanned (when still fresh) with 100 dpi resolution, in grey scale and subsequently dried to constant mass.

To measure the leaf area (L_A), the IMAGE TOOL software (developed by the University of Texas Health Science Centre in San Antonio), was used for each scanned leaf as well as for reference objects of known area to calibrate the algorithms used by the software. The sum of the L_A from 40 leaves per branch was divided by their dry mass (*i.e.*, the sum of the 40 leaves) to obtain an estimate of the leaf area/leaf biomass ratio for each branch (*i.e.*, the specific leaf area, σ, $cm^2\ g^{-1}$). Subsequently, the value of σ was multiplied by the total leaf weight, to estimate the L_A for each branch. Finally, the total L_A for each tree was calculated as the summation of the L_A from each branch.

Table 5.2: Dendrometric variables for nine destructively sampled trees. D, H, and L_A denote the diameter at breast height, total tree height and leaf area, respectively.

Tree ID	Elevation (m)	D (cm)	H (m)	L_A (m^2)	Age (years)
1	1400	41.45	25.45	122.74	73
2	1700	35.25	27.98	72.71	63
3	1880	20.92	27.1	52.82	62
4	1240	17.02	23.42	32.66	58
5	1580	9.30	12.69	9.01	58
6	1050	10.23	14.96	9.31	53
7	1630	7.28	10.6	11.09	59
8	1100	5.39	9.17	10.77	58
9	1350	5.96	10.62	12.11	50

In addition, 19 dominant and 19 suppressed trees were sampled to quantify the relationship between tree age and ANPP. Tree cores at breast height were collected from the sampled trees to determine their age and to measure the radial increment for each individual. Stem production (S_P, kg $tree^{-1}$ a^{-1}) and total tree aboveground production P_T (kg $tree^{-1}$ a^{-1}) for the last ten years and for each sampled tree were estimated through application of the empirical parameters of the allometric equations - presented in Table 4.2a - to D. Stem growth efficiency (E_S, kg $tree^{-1}$ a^{-1}) was calculated as the ratio of S_P over L_A, and total growth efficiency (E_T, kg $tree^{-1}$ a^{-1}) was calculated as the ratio of P_T over L_A.

5.2.4 Leaf area index and stand growth efficiency

Leaf area index is defined as the one-side, projected area of tree foliage in relation to the total stand area and is a dimensionless variable (L^*, m^2 m^{-2}). The L_A for the nine harvested trees was regressed against their D and the allometric relationship developed was applied to the diameter distribution of the stands presented in Table 5.1 (both for 1991 and 2001 measurements). The sum of L_A from all the trees was divided by the occupied stand area, and an estimate of L^* was finally obtained. The

stem growth efficiency of each stand (E^S, Mg ha^{-1} a^{-1}) was calculated as the ratio of stem production in the stand over its L^* (the average value of 1991 and 2001), while the total aboveground growth efficiency of each stand (E^T, Mg ha^{-1} a^{-1}) was calculated as the ratio of P^S over the L^* (the average value of 1991 and 2001).

5.2.5 Carbon isotope and foliar nutrient analysis

Sample leaves were collected from six branches - two per crown third - from each of the nine harvested trees. These sample leaves were dried to constant mass for 48 hours and were finely ground in a ball mill for further analysis. The isotope signature of carbon was expressed as $\delta\,^{13}C = (R\text{-}R_S)/R_S = R/R_S - 1$ where R_S is the molar abundance ratio $^{13}C/^{12}C$ of carbon in carbon dioxide generated from a fossil belemnite from the Pee Dee Formation which is used as a standard reference (Farquhar *et al.*, 1982). The isotope fractionation values are given in units of per mil (*i.e.*, per 1000) and the analyses were done in Boyce Thompson Stable Isotope Laboratory at Cornell Univ., USA. From the same samples, the concentration of nitrogen (N) on a per cent basis of foliage dry mass was also determined by the Kjeldahl method.

5.2.6 Statistical analysis

The ordinary least squares method and non-linear models were used to regress P^S and growth efficiency on L^*, elevation, slope and aspect, while L^* was plotted against stand basal area (B_A) and stand density (S_D, number of trees per hectare) using the SPSS software. Models were considered significant at 95%-level based on *t*-tests of the regression parameters. Differences of $\delta\,^{13}C$ values and N concentration among leaves of trees growing at different elevation and crown position were tested by two-way analysis of variance with Bonferroni's multiple comparison test (α = 0.05).

It should be noted that stand biomass of different components, P^S and L^* were underestimated in this study since trees with diameter at breast height less than 10

cm were not included in the records. However, the number per hectare of such individuals was very small (Stefanidis, person. comm.)

5.3 RESULTS

5.3.1 Analyses at stand scale

5.3.1.1 P^S and stem production

The total P^S for the 23 studied stands, presented in Table 5.1, was estimated for the ten year period (from 1991 to 2001) and averaged 7.19 Mg ha^{-1} a^{-1}. The highest P^S value of 15.71 Mg ha^{-1} a^{-1} was obtained at 1090 m above sea level, while the lowest value amounted to 1.87 Mg ha^{-1} a^{-1} at 1510 m above sea level. When P^S was regressed against elevation (U) a significant negative relationship was obtained (Figure 5.1). The coefficient of determination, R^2, was 33% and the slope was statistically different from zero ($P = 0.001$ at the 95% level).

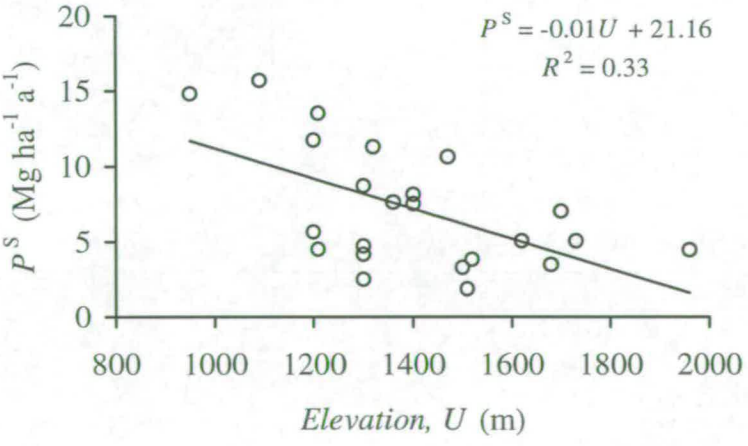

Figure 5.1: The regression line between P^S and elevation for the 23 beech stands. The ordinary least squares method was used to fit the model.

When slope (Z) was included in the P^S -elevation relationship, the R^2 was increased to 46% and the standard error of estimate was reduced from 3.36 to 3.10. The parameters were significantly different from zero and the equation obtained was:

$$P^S = -0.0978U + 0.15Z + 17.43 \qquad \text{Eq. (5.2)}$$

Including the aspect of the stand in Eq. 5.1 did not increase the value of R^2 or reduce the standard error of estimate. In addition P^S was regressed against stand basal area (B_A):

$$P^S = 1.06B_A - 16.506 \qquad \text{Eq. (5.3)}$$

with $R^2 = 0.49$ and $P<0.0001$. However, P_S was not significantly correlated to stand density (S_D, trees ha^{-1}). The stem production-elevation regression was marginally insignificant ($P = 0.06$ at the 95% level) with the upper limit of the slope range equal to zero. Neither stand basal area nor stand density was related to stem production (in both cases $R^2 < 0.05$). The production of branch biomass at the stand scale was also estimated and regressed against elevation, basal area and stand density but again no correlation was found. However, when P^S was plotted against stem production (S^S)a positive relationship was obtained (Figure 5.2).

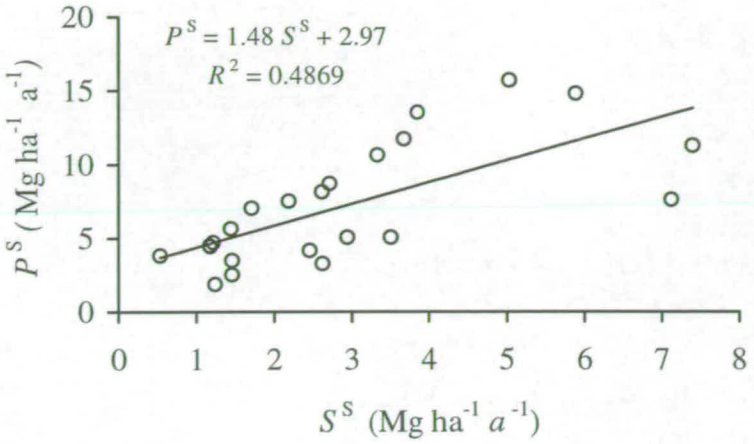

Figure 5.2: P^S regressed against the stem production (S^S) for the 23 beech stands. The ordinary least squares method was used to fit the model.

Stem production ranged from 0.53 to 7.38 Mg ha^{-1} a^{-1}and averaged 3.14 Mg ha^{-1} a^{-1}. The smallest value of beech stem production reported by Cannell (1983) was 3.5 Mg ha^{-1} a^{-1} (in Sweden) while the largest one amounted to 10.7 Mg ha a^{-1} (in Denmark). The production of harvestable boles depends not only on total net production but also on the fraction allocated to boles. Up to a point an increase in the fraction distributed into stem results in increased total biomass (Figure 5.2), since bole material does not die as early as either branches or leaves, thus turnover rates of both dry matter and energy slow down (Satoo and Madgwick, 1982). On average, 39% of P^S was allocated to crown production (branch plus foliage) while the corresponding figure for a beech stand growing in south Sweden was 60% (Nihlgard, 1972). During the 10-year study period, the aboveground net production allocated to stem, branch, and foliage was 43, 9 and 30%, respectively (figures are averages of the 23 stands) and about 12%, on average, was removed from each stand as usable timber.

*5.3.1.2 Growth efficiency and L**

To compare the productivity of trees with different size, Jordan (1971) introduced a general growth index, which is the proportion of non-photosynthetic tissue to the

photosynthetic organs, expressed in biomass units. However, since foliage biomass may vertically vary within a tree, Waring (1983) suggested that growth efficiency - measured as the ratio of stemwood production per unit of leaf area - is more sensitive to the effects of several environmental variables. The total leaf area (L_A) determined for the nine destructively sampled trees was regressed on their diameter at breast height and a very strong allometric relationship was obtained

$$L_A = 0.902D^{1.2595} \qquad \text{Eq. (5.4)}$$

with $R^2 = 0.88$ and $P < 0.001$.

Neither was the coefficient of determination increased when the correction factor (see Baskerville, 1971) was applied to this relationship, nor was the standard error of the estimate substantially decreased (from 8.84 to 8.81). The aforementioned model was applied to the diameter distribution of the 23 stands and an estimate of L^* was obtained. The total growth efficiency (E^T, computed as P^S over L^*) and stem growth efficiency (E^S, computed as stem production over L^*) was estimated and regressed against altitude. The statistical parameters for this relationship are presented in Table 5.3.

It is inferred from the Table 5.3 that the slope in E^T-elevation relationship is statistically different from zero, at 95% level, which indicates that growth efficiency for total aboveground is smaller at high altitudes. However, at stand level, stem biomass per unit leaf area does not change with elevation.

Table 5.3: Statistical parameters for **a)** E^T -elevation and **b)** E^S -elevation relationship from the 23 studied stands. The last two columns denote the range of the slope at 95% level.

	Constant	**R^2**	**Slope**	**Lower limit**	**Upper limit**
a) E^T -elevation	6.829	0.30	-0.003	-0.005	-0.001
b) E^S -elevation	3.083	0.17	-0.001	-0.003	0

E^S was also regressed on basal area and stand density but no significant correlations were obtained. E^T did not correlate with stand density but a significant relationship was obtained between E^T and basal area ($R^2 = 46\%$, $P < 0.001$). E^T varied between 0.56 to 5.2 Mg ha^{-1} a^{-1} (averaged 2.46 Mg ha^{-1} a^{-1}) while E^S varied between 0.20 to 2.54 Mg ha a^{-1} (averaged 0.99 Mg ha^{-1} a^{-1}).

The L^* ranged from 2.33 to 3.55 m^2 m^{-2} and averaged 2.81 m^2 m^{-2}over the 23 stands. Values of L^* for beech forests along a European transect (Italy, France, Germany, Denmark) fall into the range between 3.02 to 4.86 m^2 m^{-2} (Bauer *et al.*, 1997) while Nihlgard (1972) reported that a beech forest in southern Sweden attained a L^* of 2.9 m^2 m^{-2}. However, he also pointed out that when the L^* was estimated through litter fall a value of 3.4 m^2 m^{-2} was obtained. Cannell (1983), compiled the L^* estimates from forested ecosystems spanning the world and for pure beech stands the following values were reported: 3.1-3.8 in Switzerland; 7.6-7.8 in Japan; 5.9-6.7 in Germany; 4.1-6.6 in Denmark; 6.6 in France. Bartelink (1997) estimated the L^* for six even aged Dutch beech stands ranging in age from 8 to 59 years. The L^* varied from 2.79 (11-year old stand) to 7.18 (40-year old stand). More recently, Dantec *et al.* (2000) studied the spatial and temporal variations of maximum L^* of the temperate forest in Fontainebleau (France) and for beech stands L^* ranged from 2.59 to 8.06. Thus the Greek values appear to approach the lower end of this range with the lowest value of 2.33 m^2 m^{-2} recorded at 1124 m above sea level and the highest of 3.57 at 1379 m.

The L^* did not significantly relate to stand altitude ($R^2 = 0.16$, $P = 0.58$ for the linear regression and slope equalled to –0.0005), contrary to Bolstand *et al.* (2001) who reported a significantly linear L^* -elevation relationship ($R^2 = 0.58$) for southern Appalachian deciduous forests, or to slope or aspect of the stand or to any combination of the topographical variables. L^* was also regressed against the basal area (B_A, m^2 ha^{-1}) and the stand density (S_D, trees ha^{-1}) for the 23 stands and weak positive relationships are shown in Figure 5.3.

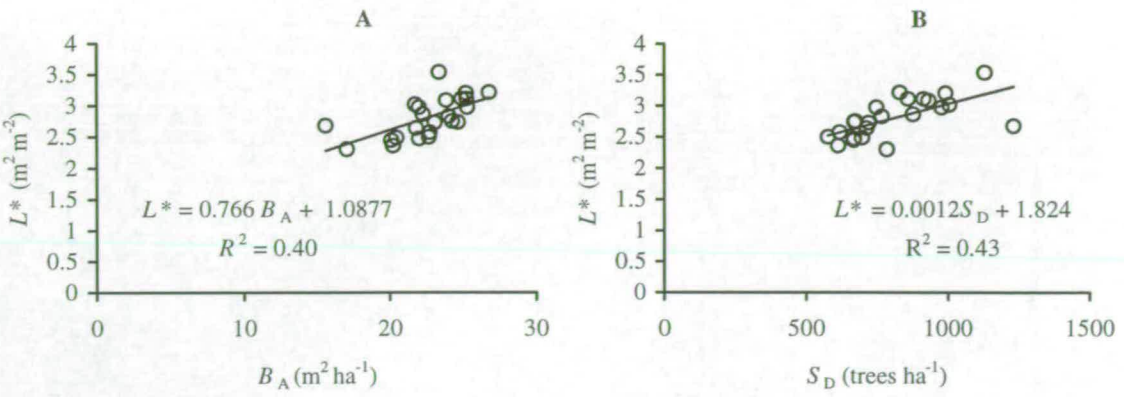

Figure 5.3: The empirical relationship for **A**) the L^*–B_A and **B**) the L^*-S_D data. L^*, B_A and S_D denote the leaf area index, the stand basal area and the stand density, respectively. The ordinary least squares method was used to fit the model.

In both regressions the slopes are significantly different from zero. Stand density and B_A were entered as the two independent variables in predicting L^* and a very strong linear regression was developed (see Table 5.4 for several statistical parameters of the model). The value of the coefficient of determination, as adjusted for the degrees of freedom, was 96% and the standard error of the estimate was 0.066.

The model is:

$$L^* = -0.337 + 1.411 \times 10^{-3} S_D + 8.909 \times 10^{-2} B_A \qquad \text{Eq. (5.5).}$$

Table 5.4: Statistical parameters for the model that relates L^* to B_A and S_D. The last two columns denote the 95% limits of the regression coefficients.

Variables	Value	St. error	Lower bound	Upper bound
Intercept	-0.337	0.147	-0.643	-0.032
Stand density	0.001411	0.0001	0.001	0.002
Basal area	0.08909	0.005	0.078	0.1

In this model, the problem of collinearity between stand density and B_A does not occur, since these two variables are not significantly related in this dataset ($R^2 < 0.02$, $P > 0.5$).

P^S was positively related to L^* consistent with other studies (Hedman and Binkley, 1988; Fassnacht and Gower, 1996; Bolstad *et al.*, 2001). In Figure 5.4A the derived relationship is depicted, while in Figure 5.4B the pooled dataset of $P^S - L^*$ pairs derived from European and Japanese beech stands is presented (from Cannell, 1983 and Nihlgard, 1972). Fruit production was excluded from the compiled values since this variable was not available.

It should be noted that for the $P^S - L^*$ model in the studied forest the slope was significantly different from zero but the intercept was not ($P > 0.05$). In Figure 5.4B, the open circle depicts the average value from the 23 studied stands, while the triangles and the crosses represent three Japanese and three German beech stands, respectively (Cannell, 1983); the squares refer to three Swedish beech stands (Nihlgard, 1972). Bolstad *et al.* (2001) reported a significant ($P^S = 1.6L^* + 0.17$, $R^2 = 0.59$) positive correlation between the two variables from studies conducted on temperate deciduous forests throughout the world.

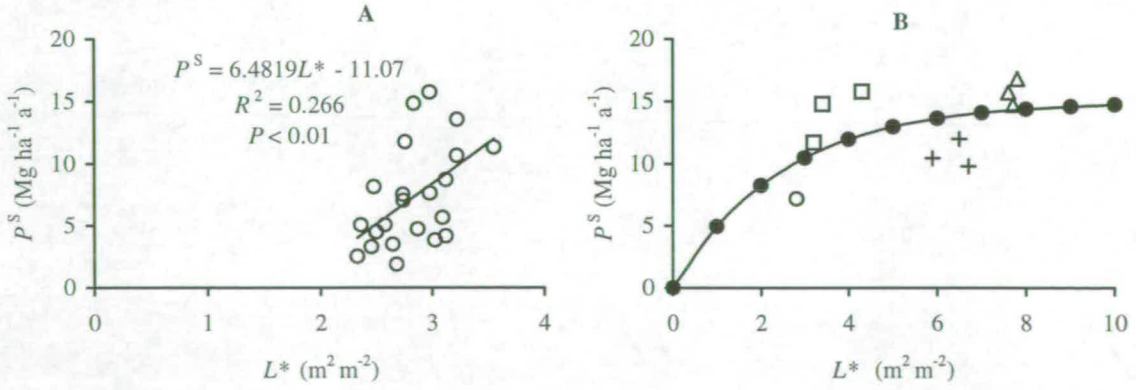

Figure 5.4: The P^S-L^* relationship for **A**) the studied forest and **B**) the pooled studies of beech stands. The open circle represents the average value from the studied forest, the triangles depict three beech stands sampled in Japan, the crosses refer to German stands and the open squares represent values from southern Sweden (data from Cannell, 1983 and Nihlgard, 1972). The closed circles represent theoretical values from Jarvis and Leverenz (1983).

The theoretical model presented by Jarvis and Leverenz (1983; Eq. 8.3 and Eq. 8.23 in their paper) was superimposed to the 'global' beech $P^S - L^*$ dataset and an average deviation of 20% between predicted and observed values was obtained. The basic assumption in this model is that the assimilation rate is linearly related to the intercepted radiation, which in turn depends on the structural properties of the canopy of which L^* dominates.

The compiled data were used to estimate E^T for beech stands growing in different environments and regressed against L^* (Figure 5.5). The obtained equation was significant at 95% level.

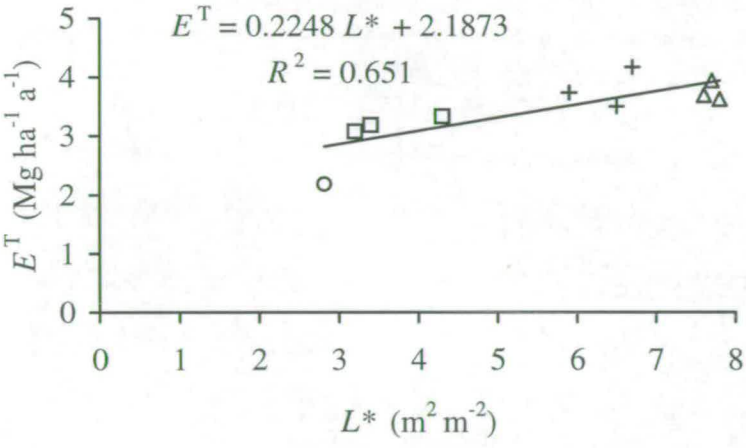

Figure 5.5: The E^T-L^* relationship for the pooled studies of beech stands. The open circle represents the average values of the studied forest, the triangles depict three beech stands sampled in Japan, the crosses refer to German stands and the open squares represent values from southern Sweden (data from Cannell, 1983 and Nihlgard, 1972).

A straightforward interpretation of Figure 5.5 would indicate that stands growing under stress conditions (as implied by the lower L^* values), are less efficient in producing organic matter per unit leaf area. One would expect that as available light to foliage decreases exponentially with increasing stand L^* (Jarvis and Leverenz,

1983), growth efficiency should decrease rapidly at higher L^* (see also Waring, 1983). However, since beech is a shade-tolerant species E^T begins to level off at values of L^* above six (Figure 5.5). The threshold value of E^T for the collected studies is 4.16 Mg ha^{-1} a^{-1} corresponding to 6.7 m^2/m^2.

5.3.2 Analyses at tree scale

5.3.2.1 P_T and tree age

Because the stands have an un-even aged structure, it is impossible to define the P^S – age relationship at the stand scale. For this purpose, the data collected from the 38 tree cores were used to quantify this relationship at the tree scale. The trees were characterised as dominant or suppressed according to their height-age relationship. The P_T for the last ten years for each tree was estimated from changes of ring width and plotted against age (Figure 5.6). As we can see in this Figure, the P_T increases rapidly following establishment, reaches a plateau at about 83 years (of more than 20 kg tree^{-1} a^{-1} for dominant trees and about 12 kg tree^{-1} a^{-1} for suppressed) and decreases abruptly at mature stages, at approximately 4 kg tree^{-1} a^{-1}.

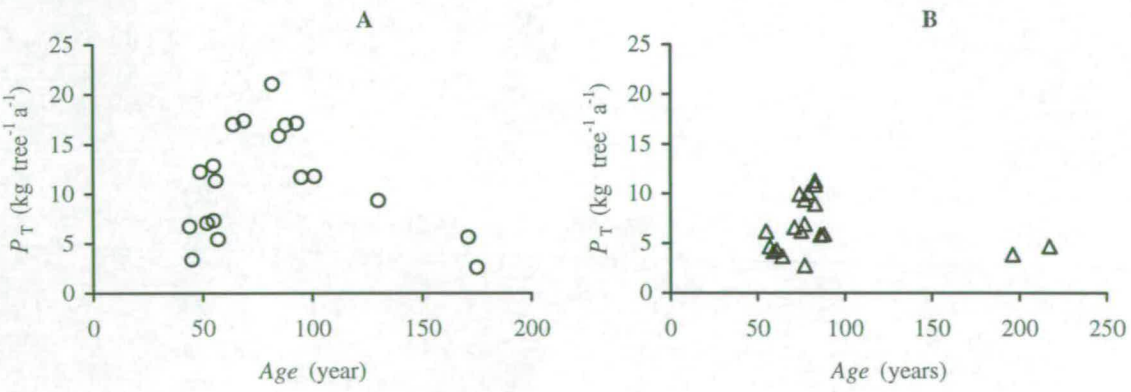

Figure 5.6: Changes in P_T as trees develop. **A**) Tree ring measurements from 19 dominant trees and **B**) tree ring measurements from 19 suppressed trees.

At this point it should be mentioned that it is extremely difficult to sample trees between 100 to 200 years because during the period 1800-1920, clearcut fellings were applied to rapidly capitalise the standing biomass. However, I used the age cores for the 196 years-old tree to obtain an estimate of the productivity potential when the suppressed trees had an age of 140 years. A value of *ca* 7.9 kg tree^{-1} a^{-1} was attained, accurately fitting the decline trend of P_T in Figure 5.6B.

Tree leaf area (L_A) exhibited the same ontogenetic trend as P_T both for dominant and stressed trees (Figure 5.7). At the age of 50 years, beech trees attained a leaf area of about 20 m^2 tree^{-1} rapidly increasing up to a threshold age. This maximum value for dominant trees amounted to 55 m^2 tree^{-1} at the age of 83 (Figure 5.7A), while the corresponding value for the suppressed was 46 m^2 tree^{-1} obtained at about the same age (Figure 5.7B). During the mature phase, the leaf area declines to about 30 m^2 tree^{-1} irrespective of the social status of the individual within the stand.

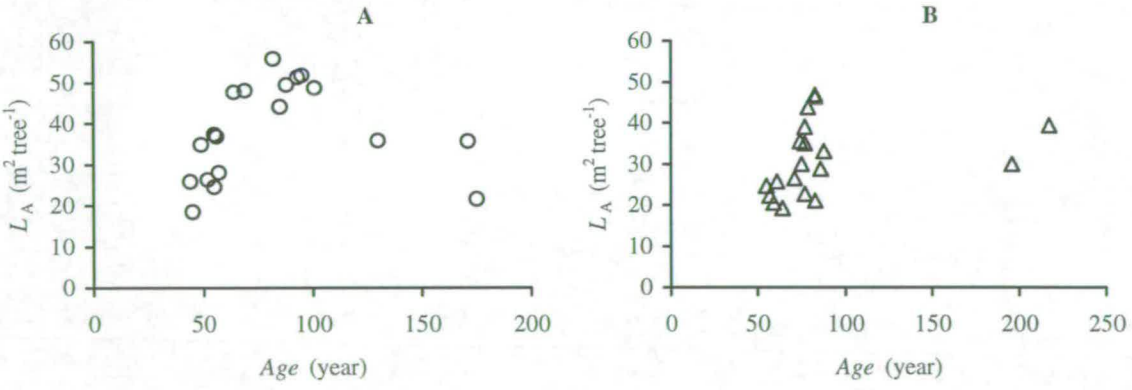

Figure 5.7: Ontogenetic trend in tree leaf area, L_A, for A) dominant and B) suppressed trees. Values for L_A did not significantly change for the dominant and suppressed trees.

Despite the profound differences in morphological and anatomical traits between dominant and suppressed trees, a strong P_T-L_A relationship is observed in Figure 5.8.

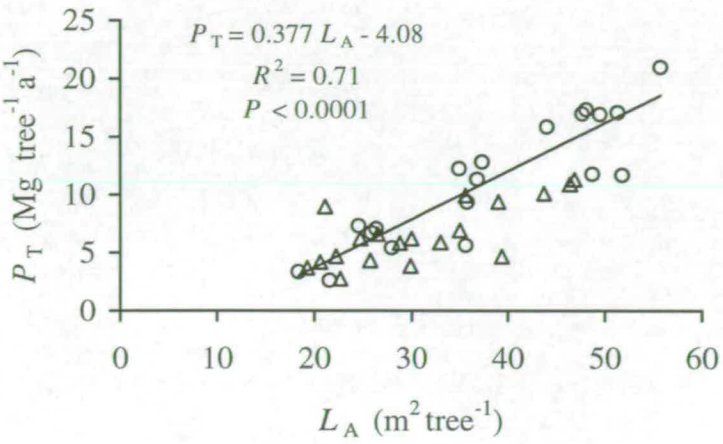

Figure 5.8: P_T vs. L_A for 19 dominant (open circles) and 19 suppressed (open triangles) trees. A linear regression was fitted irrespective of the social status. The majority of the dominant trees fall above the regression line, which indicates that they produce more aboveground organic matter for a given L_A value, than the suppressed trees.

Stem production (S_P) calculated for the last 10 years was plotted against tree age and a pattern similar to the ontogenetic changes of P_T was obtained (Figure 5.9).

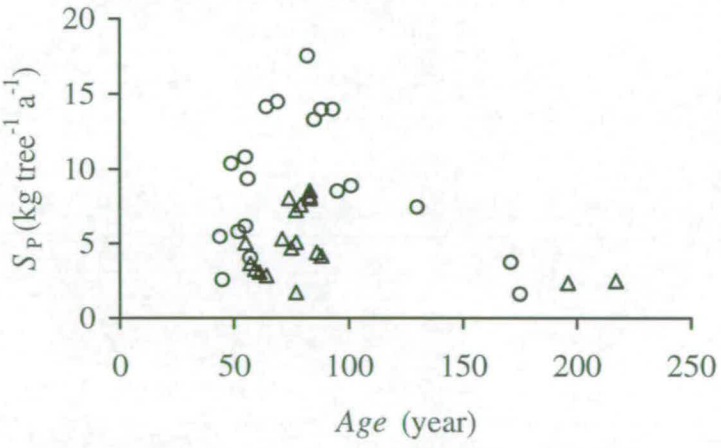

Figure 5.9: S_P vs. tree age for 19 dominant (open circles) and 19 suppressed (open triangles) trees. The majority of the dominant trees attained a larger S_P value from 50 to 100 years than the suppressed trees. At the mature phase, the S_P is similar for dominant and suppressed trees.

According to Figure 5.9, the stem productivity of dominant trees (open circles) culminates at 82 years with a value of 17 kg tree^{-1} a^{-1}, while suppressed individuals (open triangles) produce about half of this amount (8.15 kg tree^{-1} a^{-1}); at the later stages of tree life, growth of stem wood is quite similar for dominant and suppressed trees (*ca* 3 kg tree^{-1} a^{-1}). Neither stem efficiency (E_S, kg tree^{-1} a^{-1} m^2) nor total growth efficiency (E_T, kg tree^{-1} a^{-1} m^2) were correlated to tree leaf area but a very strong linear relationship was obtained when E_S was regressed on E_T for the 38 sample trees (Figure 5.10). The intercept was significantly different from zero while the slope ranged from 0.951 to 0.993. The efficiency of stem growth varied between 0.06 to 0.38 kg tree^{-1} a^{-1} m^2 and averaged 0.19 kg tree^{-1} a^{-1} m^2, while the range of growth efficiency of total aboveground biomass was from 0.11 to 0.42 kg tree^{-1} a^{-1} m^2 with an average value of 0.24 kg tree^{-1} a^{-1} m^2. The maximum values for stem and total efficiency were obtained for a suppressed 83 years-old tree growing at 1520 m altitude above sea level with a diameter at breast height equal to 14.26 cm. The tight relationship in Figure 5.10 implies that trees allocate the same proportion of organic matter produced per unit leaf area to stem growth, irrespective of the factors limiting tree growth and development.

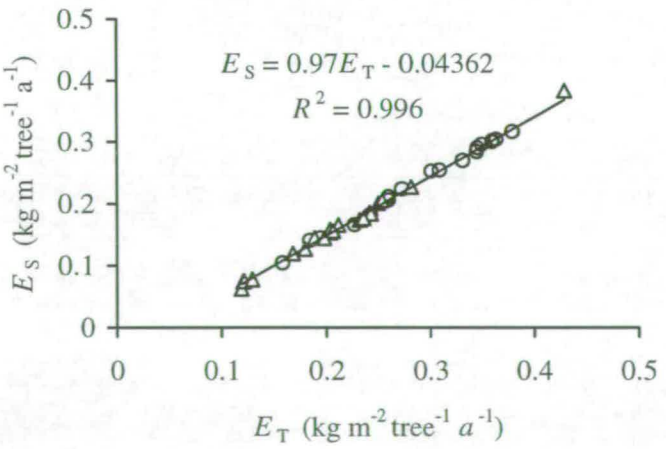

Figure 5.10: Stem efficiency (E_S) vs. total growth efficiency (E_T) for 19 dominant (open circles) and 19 suppressed (open triangles) trees. The ordinary least squares method was used to fit the regressed model.

5.3.2.2 Specific leaf area

Since the study trees originated from uneven-aged stands, canopy depth could not be used as a surrogate variable for the effects of shading on the physiology of the harvested trees. Thus the analyses presented in the following Sections, were based on absolute sampling height above ground. For comparison, analyses based on crown depth are presented in the Appendix (Table A2 through Table A4). The nine destructively harvest trees (Table 5.2) were used to study the variation of σ within the beech canopy and across the elevation gradient. Patterns of σ were similar among the sample trees. Values of σ increased from an average of 183.61 $cm^2\ g^{-1}$ in the top canopy layer to an average of 205.40 $cm^2\ g^{-1}$ in the middle third of the crown and to an average of 251.39 $cm^2\ g^{-1}$ in the lower canopy layer.

Specific leaf area values for the upper canopy of beech trees sampled across a European transect (from Italy to Denmark) averaged 189 $cm^2\ g^{-1}$ with a standard deviation of 4.4 $cm^2\ g^{-1}$ (Bauer, 1997) consistent with the results obtained from this study. The height of the collected leaves was plotted against the pooled σ values and a negative significant relationship was obtained (Figure 5.11). The coefficient of determination was about 60% and the slope was significantly different from zero ($P<0.0001$). Cermak (1998) studied the leaf distribution of large trees in southern Moravia and he also found close relationships between σ and canopy height for broadleaf species, that corresponded to changes in leaf thickness and decreasing irradiance within the crown. It is well known that leaves in the shade receive less total incoming radiation and consequently are thinner than leaves on the same tree exposed to direct light. Shade leaves also tend to be larger and have fewer well-defined mesophyll layers and fewer chloroplasts than their sunlit counterparts (Stern, 2000).

The nine sampled trees (Table 5.2) were classified into three altitudinal elevation groups (lower, middle, upper) and a univariate analysis of variance was done to

determine whether specific leaf area values exhibited altitudinal variations when absolute sampling height is taken into account (Table 5.5).

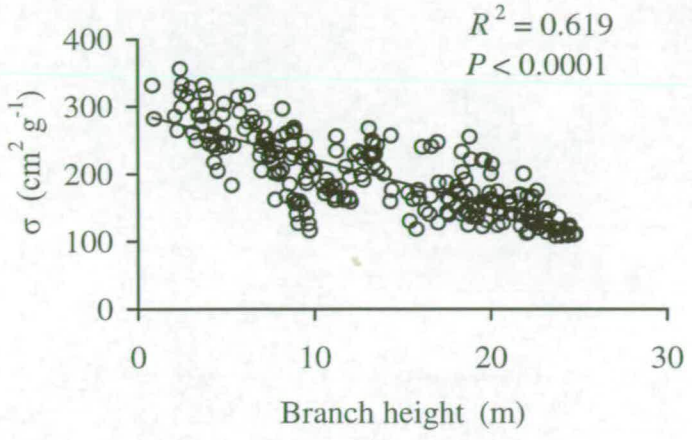

Figure 5.11: Branch height plotted against the pooled σ values. The ordinary least squares method was used to fit the regressed model.

Table 5.5: The analysis of variance for the σ values calculated for the nine sampled trees collected from three elevation classes. The model is $\sigma = I + j + E_C$ where I denotes the intercept, j the sampling height and E_C the elevation class, respectively. The coefficient of determination is 0.68.

	Sum of squares	*df*	*Mean square*	*F*	*P*
Corrected	71424.88	3	23808.29	34.6	< 0.001
Intercept	356211.86	1	356211.86	517.77	< 0.001
HEIGHT	17730.14	1	17730.14	25.77	< 0.001
ELEVATION	33191.44	2	16595.72	24.12	< 0.001
Residual	34398.50	50	687.97		
Total error	1878484	54			

The same analysis was done on crown depth data and the results are presented in the Appendix (Table A2).

The estimated average and marginal means of σ for different elevation classes, when differences in absolute sampling height were taken into account, are presented in Table 5.6.

Table 5.6: Estimated average and marginal means of σ values for different elevation class calculated for the nine sample trees in three groups.

Elevation	*Mean*	*Std. Error*	*Lower*	*Upper*
Lower	211.73	6.219	199.238	224.222
Middle	183.28	6.29	170.651	195.921
Upper	148.53	6.45	135.575	161.487

Table 5.6 shows a significant decrease of σ values with increasing altitude is presented in Table 5.6, when absolute sampling height of leaves is taken into account. Thus, at 95% level, the σ was smaller near the top of the mountain than in the bottomlands. Vitousek *et al.* (1988) reported a similar trend in σ for sunlit leaves at a Hawaiian montane rainforest and attributed this pattern to nutrient limitation or low water availability at higher elevations. Jose and Gillespie (1996) studied the foliage variation along a moisture gradient in central USA forest communities and concluded that σ decreased with decreasing moisture availability.

5.3.2.3 Carbon isotope and foliar nitrogen

An analysis of foliar carbon isotope and nitrogen concentrations took place for the nine harvested trees. According to previous analysis (Figure 5.1), aboveground net primary production significantly decreased with elevation. To illustrate which factors may impose such limitations in production at higher elevation, the carbon isotope data and the foliar nutrient analysis of the sampled trees were used.

Carbon isotope

The $\delta^{13}C$ values for the six sampled branches on the nine sampled trees were averaged for each tree and regressed against elevation (Figure 5.12).

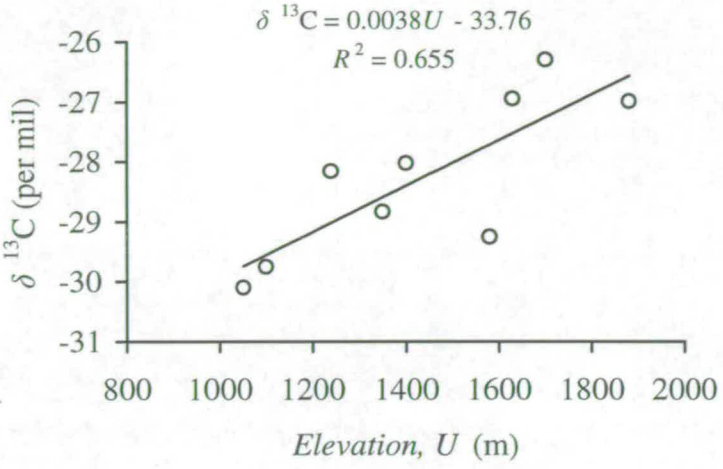

Figure 5.12: Regression of average tree $\delta^{13}C$ values against elevation for the nine sampled trees (Table 5.2). The least squares method was used.

The elevation explained more than 65% of the variability in the composition of carbon isotope in leaves. The slope ranged from 0.001 to 0.006 and averaged 0.0038 ($P = 0.008$). The average value for the intercept was –33.76 ‰ and significantly different from zero ($P = 0.0001$). However, one could argue that, following Francey and Farquhar (1982) and Schleser and Jayasekera (1985), the interpretation of the pooled regression (Figure 5.12) is not based on sound analysis since the sampled trees did not have the same stature (Table 5.2). Changes in stem hydraulic conductivity and branch length with height (Waring and Silvester, 1994) are expected to have an influence on the delta values of the sampled trees.

To robustly test the relationship between delta values and crown position, the raw data from the 54 samples were used in a linear regression. The natural ratio of stable carbon isotopes was regressed against the absolute height above ground. The R^2 was

34% and the slope and the intercept were significantly different from zero at the 95% level (Figure 5.13).

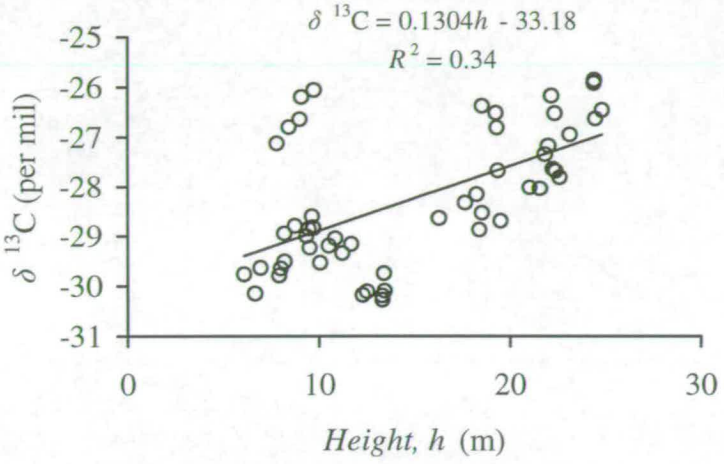

Figure 5.13: Regression of average tree $\delta^{13}C$ values against height above ground. The least squares method was used to fit the model.

Table 5.7: The analysis of variance for $\delta^{13}C$ values calculated for the nine sample trees collected from three elevation classes. The model is $\delta^{13}C = I + j + E_C$ where I denotes the intercept, j the sampling height and E_C the elevation class, respectively. The coefficient of determination is 0.80.

	Sum of squares	*df*	*Mean square*	*F*	*P*
Corrected	76.98	3	25.66	65.27	< 0.001
Intercept	5896.36	1	5896.36	14996.63	< 0.001
HEIGHT	11.11	1	11.11	28.27	< 0.001
ELEVATION	44.16	2	22.08	56.15	< 0.001
Residual	19.65	50	0.393		
Total error	43219.14	54			

A univariate analysis of variance was also carried out to determine whether delta values exhibited altitudinal variations when absolute sampling height is taken into account (Table 5.7). The same analysis based on crown depth data took place and the results are presented in the Appendix (Table A3). The estimated average and marginal means of delta values for different elevation classes, when differences in absolute sampling height were taken into account, are presented in Table 5.8.

Table 5.8: Estimated average and marginal means of $\delta^{13}C$ values for different elevation class calculated for the nine sample trees.

Elevation	*Mean*	*Std. Error*	*Lower*	*Upper*
Lower	-29.24	0.149	-29.54	-28.94
Middle	-28.55	0.15	-28.85	-28.25
Upper	-26.97	0.154	-27.28	-26.66

Less negative values of $\delta^{13}C$ with increasing altitude are shown in Table 5.8. Several studies have reported altitudinal shifts in $\delta^{13}C$ at the intraspecific level (Körner *et al.*, 1988; Vitousek *et al.*, 1990; Körner *et al.*, 1991; Sparks and Ehleringer, 1997). The general increase in ^{13}C content with altitude indicates that the overall discrimination against the heavy isotope is reduced at high elevation. However, Körner *et al.* (1988) concluded that the altitudinal variation of the atmospheric isotope composition cannot account for the observed discrimination in leaves. In other words, atmospheric variation in $\delta^{13}C$ constitutes only a minor portion of the differences obtained in plant tissue composition and other physiological reasons should be found to explain this trend.

Foliar nitrogen

Leaf nitrogen concentration was used to obtain the nitrogen content (measured in g) for the leaves of the 54 sample branches. The nitrogen content values per unit leaf area (N_A, g cm^{-2}) and per unit leaf mass (N_M, g g^{-1}) were also calculated. The 54 sample value of nitrogen for leaves on the six branches per tree were used to

investigate the effects of sampling height and elevation on leaf nitrogen content, expressed as N_A and N_M. The results are presented in Table 5.9.

Table 5.9: The analysis of variance table for the influence of sampling height and elevation on the values of **A**) N_A (g cm^{-2}). The model is $N_A = I + j + E_C$ where I denotes the intercept, j the sampling height and E_C the elevation class, respectively. The coefficient of determination is 0.74. **B**) N_M (g g^{-1}). The model is $N_A = I + j + E_C$ where I denotes the intercept, j the sampling height and E_C the elevation class, respectively. The coefficient of determination is 0.48. Data from the nine sample trees.

A: *Nitrogen per unit area*	***Sum of squares***	***df***	***Mean square***	***F***	***P***
Corrected	8.405×10^{-8}	3	2.802×10^{-8}	48.159	< 0.001
Intercept	2.75×10^{-8}	1	2.75×10^{-8}	47.27	< 0.001
HEIGHT	3.305×10^{-8}	1	3.305×10^{-8}	56.808	< 0.001
ELEVATION	2.341×10^{-8}	2	1.171×10^{-8}	20.12	< 0.001
Residual	2.909×10^{-8}	50	5.818×10^{-8}		
Total error	1×10^{-6}	54			

B: *Nitrogen per unit mass*	***Sum of squares***	***df***	***Mean square***	***F***	***P***
Corrected	3.214×10^{-4}	3	1.071×10^{-4}	15.47	< 0.001
Intercept	1.767×10^{-3}	1	1.767×10^{-3}	255.3	< 0.001
HEIGHT	2.292×10^{-4}	1	2.292×10^{-4}	33.11	< 0.001
ELEVATION	1.994×10^{-5}	2	9.971×10^{-6}	1.44	> 0.20
Residual	3.461×10^{-4}	50	6.923×10^{-6}		
Total error	2.57×10^{-2}	54			

The crown layer analysis of N_A and N_M is presented in the Appendix (Table A4). Table 5.9B shows that there was no significant difference for the nitrogen content per unit leaf mass across the elevation gradient. However, N_A varied in relation to

altitude (Table 5.9A). The average N_A values for trees located in the lower, middle and upper elevation zone was 1.081 x 10^{-4}, 1.19 x 10^{-4} and 1.593 x 10^{-4}, respectively. The N_A was significantly different between lower and upper elevation, as well as between moderate and upper elevation, but not between lower and medium elevation. The absolute sampling height had a significant effect on both variables (*i.e.*, N_A and N_M).

The carbon isotope ratios (δ ^{13}C) were plotted against N_A and N_M and the least squares method was used to fit a linear model. A strong (R^2 = 68%) positive relationship was obtained only with the N_A variable (Figure 5.14), consistent with the results reported by Körner and Diemer (1987; data collected from herbaceous species growing in Alps), Sparks and Ehleringer (1997; data from deciduous riparian species) and Hultine and Marshall (2000; data for *Pinus contorta*).

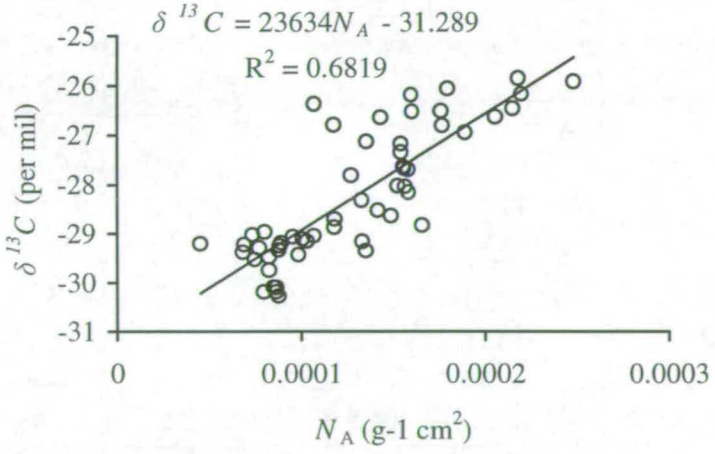

Figure 5.14: Regression of δ ^{13}C values against N_A. The least squares method was used to fit the model.

Finally, δ ^{13}C was regressed against σ and the negative linear relationship (R^2 = 68%, P = 0.0001) is depicted in Figure 5.15. Vitousek *et al.* (1988) found a similar trend for foliar samples from *Metrosideros polymorpha* species growing in a Hawaiian

montane rainforest. Similar results were also reported by Hultine and Marshall (2000), who studied four coniferous species in USA.

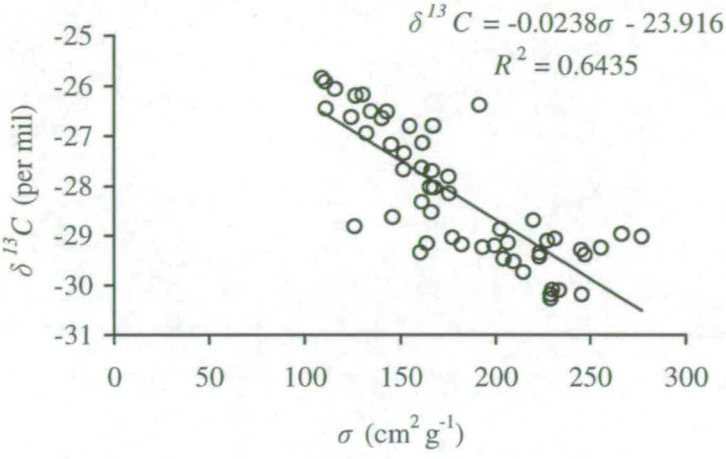

Figure 5.15: δ ^{13}C values as a linear regression of σ. The least squares method was used to fit the model.

5.4 DISCUSSION

The variation of the aboveground net primary production in a natural regenerated beech forest has been investigated in this Chapter. Data collected from twenty-three plots were analysed to obtain information at the stand scale, while nine trees were destructively harvested to determine the effects of environmental variables on ANPP and growth efficiency. This study should be considered as preliminary and further investigation is required to increase our understanding of the topoclimatic influences on potential productivity of the beech ecosystems in Greece.

P^S variations along the elevation gradient (as depicted in Figure 5.1), are consistent with results from southern Appalachian deciduous forests (Bolstand *et al.*, 2002). P^S decreased as elevation increased and this relationship may have been caused by many factors. Decrease in growing season length with elevation (Bolstand *et al.*, 2002), lower mean annual temperatures at higher altitude (Leith, 1975), and decline of foliar nutrient concentrations with increasing elevations (Vitousek *et al.*, 1888) are reported to significantly affect P^S – elevation relationship. The positive linear relationship between P^S and L^* was found to be significant for the studied forest, but not for the global compilation of beech ecosystems (see Figure 5.4). Jarvis and Leverenz (1983) had listed the L^* as the most important canopy property for radiation interception and consequently of plant production while a similar trend of increasing P^S with increasing L^* has also been documented in many empirical studies (Whittaker, 1966; Hedman and Binkley, 1988; Fassnacht and Gower, 1996; Bolstad *et al.*, 2001; to name but a few). The existence of a relationship between these variables mainly derives from the fact that leaf area is the surface which controls, to a large extent, energy (sunlight) and matter (carbon and water) fluxes in plant biochemical processes.

The low L^* values obtained from the studied forest could either be attributed to the dry Mediterranean climate and/or to the uneven age structure of the stands. In the vast majority of the European studies (Nihlgard, 1972; Cannell, 1983; Bartelink, 1997; Bauer *et al.*, 1997; Dantec *et al.*, 2000) the reported L^* was estimated for mature even-aged stands whose canopy was in a 'steady state' condition. On the other hand, the studied stands exhibit a dynamic process of regeneration-mortality mechanism where gaps created by fallen trees, are immediately replaced by seedlings growing under the shade of adults, which compete with mature and very old trees for acquisition of sunlight. Thus, it is very common to meet trees of all sizes within a stand, which in turn result in small L^* values.

Long and Smith (1990), explained the increases in productivity by higher L^* with differences in stand structure. L^* was very strongly related to basal area and stand

density (Eq. 5.7 and Table 5.4), implying that silvicultural regimes may be adjusted so as to obtain maximum leaf area in each stand and in turn to maximise wood production on a per hectare basis. At the stand scale about 49% of the P^S was allocated to stem production while 9 and 30% was partitioned to branches and foliage, respectively.

Total growth efficiency (E^T) varied across the elevation gradient but stem growth efficiency (E^S) did not (Table 5.3). The variation of E^T indicates that per unit of L^*, beech stands produce more aboveground dry biomass at sites located at lower elevation than stands growing at the upper limit of the forest. Waring (1983) suggested that when compared at similar levels of L^*, E^T could provide a measure of the relative importance of various environmental factors to produce organic matter. As depicted in Figure 5.5, even though the Greek and the Swedish beech ecosystems have about the same L^* (difference is less than 0.4 m^2/m^2), the productive capacity of Greek stands are smaller (2.18 Mg ha^{-1} a^{-1}) than the Swedish ones (3.10 Mg ha^{-1} a^{-1}). A possible explanation for this difference in growth efficiency may be attributed either to abiotic factors (climate, soil moisture and nutrient availability) and/or to human induced disturbances (the history of the two forests is believed to be different). Jose and Gillespie (1996) studied the aboveground production efficiency of mixed-hardwood forest communities along a moisture gradient in the central USA and found that E^T was influenced by soil moisture and foliar nutrients.

Because of the uneven age structure of the beech forest, it was impossible to study the P^S – age relationship at stand scale. Thus, cores taken from 38 trees located across the studied ecosystem were used to construct the dynamics of aboveground production through time. The obtained trend (Figure 5.6) is quite similar to the one presented by Ovington (1957) for Scots pine trees. Tree production increases slowly at first until it produces enough foliage, roots and other tissues to allow rapid assimilation. Then, it grows rapidly during the grand period of growth as the foliage and absorptive roots grow more rapidly than the respiring tissue. After the culmination of growth (mature trees), the total respiration of different tree

compartments becomes a larger fraction of the assimilated photosynthates (very old trees). Eventually, net primary production drops since a large proportion of assimilates is consumed for the maintenance of the living tissue. Assmann (1970), reported that the allocation of photosynthates among respiration, root and foliage growth, and stem growth, varied for ash trees with different vigour. In dominant trees, about 42% of gross photosynthesis was allocated to stem growth while only 8% was allocated to stem growth for suppressed trees (see also Figure 5.9). This mechanism may explain the difference in P_T between dominant and suppressed trees in the study forest (Figure 5.6A versus Figure 5.6B). The leaf area of the sample trees followed a similar ontogenetic trend as P_T (Figure 5.7) which largely explains the close relationship between P_T and tree leaf area (Figure 5.8).

Since L^* did not significantly change across the study beech ecosystem, analysis at leaf level took place in order to explain the P^S variation along the elevation gradient. It is well-known that nitrogen concentration (Birk and Vitousek, 1986; Stern, 2000) and water stress (Dupouey *et al.*, 1993; McNulty and Swank, 1995; Stern, 2000), may limit the aboveground production of forest ecosystems. To demonstrate which factors may affect primary production in the study ecosystem, surrogates variables such as σ, nitrogen content and $\delta\ ^{13}C$ signature for six branches, collected from each of nine trees, were determined. According to Hultine and Marshall (2000),

'Stable isotope composition, reflects the balance between mesophyll demand for carbon dioxide against the diffusive supply through the stomata'.

According to Figure 5.13 the trees located at higher elevations had less negative $\delta\ ^{13}C$ values, indicating that are possibly more stressed than the ones growing in the bottomlands. The obtained $\delta\ ^{13}C$ signal may explain the negative trend of P^S in relation to elevation (Figure 5.1). Why did $\delta\ ^{13}C$ values increase with elevation? As we can see in Table 5.9, N_A was higher at the top of the mountain than at the bottomland (see also Table A4). The close positive relationship between $\delta\ ^{13}C$ and N_A (Figure 5.14) may be a possible explanation of the altitudinal trend of carbon discrimination. The correlation between the two variables is ascribed to the fact that

most of the leaf nitrogen is bound in photosynthetic enzymes (Stern, 2000), and therefore higher nitrogen per unit leaf area increases CO_2 demand at the sites of carboxylation (Körner and Diemer, 1987; Körner, 1989; Sparks and Ehleringer, 1997), thereby reducing intercellular CO_2 concentration and, in turn, discrimination against ^{13}C.

Moreover, $\delta\ ^{13}C$ was also tightly coupled with σ (Figure 5.15) in accordance with Vitousek *et al.* (1990) and Hultine and Marshall (2000). Vitousek *et al.* (1990) suggested that increased $\delta\ ^{13}C$ values in thicker leaves are due to the longer diffusive path to the sites of carboxylation. An alternative explanation could be that higher σ indicates broader leaves per unit mass which implies more stomata per unit area supplying the same photosynthetic machinery per unit mass as their narrow counterparts. Analysis of variance indicated that the σ values decreased with elevation (Table 5.5 and Table 5.6), which in turn implies an increase in N_A and a reduction of the discrimination against the heavy C isotope (Figure 5.15).

Since wind speed increases with elevation (Grace, 1983) the coupling effect of the stomata is greater at the top of the mountain so the potential water loss can be regulated by reducing specific leaf area. Another possible explanation for small σ values at higher altitudes could be based on the biomechanics of tree crowns. Higher leaf area per unit mass results in greater dynamics loads at higher wind speeds, which in turn imposes stability risk to the trees. Thus, reducing σ can minimise the effects of wind loadings at the upper elevations.

Since the studied ecosystem extends from *ca.* 900 to 1900 m, we would expect higher precipitation at upper altitudes, which in turn indicate higher productivity for the stands located near the top of the mountain. However, the slopes at those elevations are much steeper (40-60%) than at lower sites (10-20%), indicating a different degree of surface runoff and water percolation between bottomlands and highlands. Consequently, soil water availability is considered to be greater at low elevation sites, and thus trees produce more organic matter on a per hectare basis.

Harrington *et al.* (1995) had investigated the growth of *Acacia koa* species in Hawaiian forests and reported that aboveground productivity was limited more by water than by soil nitrogen availability or nitrogen uptake. However, constant L^* values across the forest imply that neither soil moisture nor nitrogen availability are likely to differ among sites. Appropriate datasets had not been collected in order to thoroughly test this hypothesis for the study ecosystem, but such questions may be addressed for further research.

Finally, it should be pointed out that an important component missing from this study was the belowground (coarse and fine roots) dry biomass dynamics. Root biomass estimation is a very laborious procedure rarely measured for tree species (for some exceptions see Nihlgard, 1972; Deans *et al.*, 1996; Ottorini and Le Goff, 1998). Cannell (1989), and Cannell and Dewar (1994) reviewed the principal concepts that have been put forward to model carbon allocation in plants under biomechanical and physiological constraints. One of the main conclusions drawn from these studies is that a functional and structural equilibrium exists for carbon absorption, water uptake and mechanical stability in plants. Thus, assimilates are allocated to shoots if several factors limit carbon intake or light interception and to roots when nutrient or water limitation and dynamic forces are detected. Accordingly, root biomass and belowground production are believed to be larger in the upper limit of the beech ecosystem, assuming that wind speed is greater at these sites (Grace, 1983) and that no variability exists for soil water and nutrient across the forest. However, whether these hypotheses hold true will have to be empirically verified.

6. GENERAL DISCUSSION

This Thesis consists of two parts, the theoretical (Chapter 2 and Chapter 3) and the empirical one (Chapter 4 and Chapter 5). Chapter 2 introduced theoretical aspects of first engineering principles applied to plant biology in order to explain the interrelationships among the linear dimensions of forest trees. A new model was also formulated to understand the effects of biomechanical constraints on the scaling of size-shape relationships in terrestrial trees. In addition, analysis based on fractal geometry (the 'reductionist' model) was used in order to understand the meaning of the parametric values in *H-D* and *M-D* allometries while the applicability of the 'reductionist model' in biomass studies was also examined. In Chapter 3 a novel method for simplifying allometric analysis of forest trees and stands (called SSS) was presented. The SSS approach was based on simple assumptions made by the model I regression. Empirical allometric relationships among dendrometric variables for *Fagus moesiaca* Cz. trees growing in Vermio Mountain, Northern Greece were developed in Chapter 4. These equations were applied in the study forest and estimations of aboveground net primary productivity were finally reported in Chapter 5. In the following two Sections a more detailed discussion for the theoretical and empirical part is presented.

6.1 ON THE THEORETICAL PART

Allometric relationships in Biological sciences have been studied for about a century. Theoretical and quantitative work in scaling analysis initiated with the famous books of D'Arcy Thompson *On Growth and Form* (1917), and Julian Huxleys' *Problems on Relative Growth* (1932). Influential syntheses and reviews by Gould (1966; 1971), Leopold (1971), McMahon (1973; 1975) and Calder (1984) laid the foundation for the current state of the field. Quite recently the Santa Fe Institute in the Sciences of Complexity held a symposium on *Scaling in Biology* and views presented in the meeting were subsequently published in 2000 (Brown and West, 2000).

Scaling analysis is vital to understanding biology in general and botany in particular (Niklas, 1994), either from the point of view of the 'bio-physical force that steers evolution' or from that of the 'trial-and-error of natural selection' process. The first attempt to study the relationship between tree height and diameter was initiated by Greenhill (1881) and thereafter first principles derived from the engineering theory were applied in order to predict the interrelations among the linear dimensions of trees and plants (Gere and Carter, 1963 cited in Holbrook and Putz, 1989; McMahon, 1973; McMahon and Kronauer, 1976; King and Loucks ,1978; Holbrook and Putz, 1989 Niklas, 1992; Niklas, 1994; Sterck and Bongers, 1998). However, according to Grace (1997) the 'pipe model' (Shinozaki *et al.*, 1964a and 1964b) approach is still the most widely cited model for whole-plant structure, although several authors have pointed out some problems with its assumptions (*e.g.*, Tyree and Ewers, 1991). Recently, West *et al.* (1999) developed a theoretical model (WBE) based on simple geometric rules to predict several functional-structural relationships within different plant organs and among individuals growing in similar environment.

According to WBE model, constant allometries can very accurately describe the scaling relationships within and among trees (Enquist *et al.*, 1998; Enquist *et al.*, 1999; West *et al.*, 1999; Enquist *et al.*, 2000; Enquist and Niklas, 2001). However, empirical studies (Niklas, 1999; Chambers *et al.*, 2000; Chapter 2 and Chapter 3) and theoretical arguments (Magnani *et al.*, submitted) have questioned the global applicability of the WBE model. This model predicts a universal value for the slope in Eq. 2.2 equal to 2.67, but analysis of the world-wide compilation of biomass allometric relationships indicated that, on average, the slope is smaller than the predicted one (Figure 2.7). Why did WBE fail to capture the variability in *M-D* allometries?

The WBE model uses simple assumptions about the transport of essential materials through vascular networks while the predicted branching fractal structure is believed to supply resources to all parts of a three-dimensional body (Enquist *et al.*, 2000).

However, many studies have demonstrated that trees should not be described within the domain of Euclidean geometry, implying that they are not 3D ideal objects (Mandelbrot, 1983; Zeide, 1991; Zeide and Gresham, 1991; Zeide and Pfeifer, 1991; Berezovskava *et al.*, 1997; Horn, 2000). In order to describe mathematically the branching system of tree crown, the authors used simple geometrical rules about the relationship of length and diameter between parent and daughter branches, as well as for vessel tube radii between parent and daughter branches. Their model predicts that stationary laws (*i.e.*, constant scaling) may explain the bifurcation process during tree ontogeny, which eventually results in a volume-filling crown (at least in the periphery of the tree canopy). However, such a structure would not leave any space for photosynthetic machinery (*i.e.*, leaves) to be developed, and this immediately contradicts the present understanding of plant structural and functional properties.

Apart from the physiological caveats of the WBE model, the predicted canopy structure is considered to be an ideal fractal (which can be derived with replication of the same geometrical algorithm through time) and cannot describe the branching pattern of a real tree which is a natural fractal (Mandelbrot, 1983; Berezovskava *et al.*, 1997; Horn 2000). The distinction between the two categories of fractal objects is whether randomness is allowed to play a role in the growth and development of the new generation of branches. Such a procedure is missing from the model presented by West *et al.* (1999). The WBE model contains a 'self-contradicted' element since the predicted variables overcome in number (at in qualitative terms) the mathematical parameters used for the development of the model. For example, an appropriate mathematical manipulation of simple geometrical rules cannot be the only factor affecting metabolic rate or branch resistance of a tree. If we believe that immutable laws of cause and effect should describe the real phenomena of the natural world then the geometrical analysis presented by West *et al.* (1999), should not be considered the cause of the interdependency of tree functional and structural characteristics. Environmental variables can have a large impact both on the morphology and physiology of trees. However, procedures to incorporate environmental influences in the model are not available. In conclusion, their model

should be viewed as a preliminary step to predict the interrelationships between tree structure and function, while basic assumptions in their approach should also be modified for advancing understanding in plant biology.

Theoretical analyses of tree scaling relationships have mainly focused, so far, on the study of allometric exponents, either implying that the scaling intercept has no meaning or that its interpretation is much more difficult. White and Gould (1965) proved that both scaling parameters play an important role in biological phenomena (at least in zoological - related processes). However, in their attempt to interpret the relationship between the scaling parameters (a and b in Eq. 2.1), they concluded that a biological meaning cannot be inferred from this dependency. They rejected the biological significance of a-b relationship because of implications derived from mathematical artefacts. However, I have shown in this Thesis that these artefacts can be taken into account and consequently a biomechanical model was developed (Eq. 2.4b) to explain variability in the empirical a-b relationship.

A very interesting outcome of the model is that the parametric values describing the M-D relationships do not follow 'random' rules but seem to comply with restrictions imposed by the mechanical properties of wood structure. The biomechanical model (Eq. 2.4b) was built upon the assumption that trees attain appropriate dimensions so as not to collapse under their own weight, and empirical data verified this assumption (see Table 2.5). Irrespective of tree species or growing conditions, M-D relationship seems to obey a universal property. A simple question arising from the relationship between a and b is why a particular stand 'selects' a specific pair of a-b values and not another one. An immediate answer may indicate that stand structure plays a central role in tree shape and in turn in M-D allometry. Other factors, such as different allocation patterns and/or genetically driven processes could also constitute a potential explanation. However, an analysis of b values for 27 tree families indicated that no significant differences existed among them (Figure 2.10).

One of the weaknesses of the biomechanical model is that the flow of materials, involved in energy exchange, as well as the tree hydraulic properties were not taken into consideration during its development. Since biomechanical and hydraulic properties are not mutually exclusive, the next step would be to merge them and test whether such an approach may explain more of the variability in *M-D* allometries.

Since the empirical values of the allometric parameters in *M-D* equations are restricted by the necessary correlation between a and b, and not affected by random processes, it was clear that low-level information may help us to simplify *M-D* allometry. Thus, the SSS method was developed in order to predict dry aboveground biomass at stand scale (Chapter 3). In the SSS approach, the world-wide database of the empirical equations that relate aboveground biomass to stem diameter was used in conjunction with the statistical properties of allometric equations in order to obtain biomass predictions with minimum effort (harvest of small trees is only required). The SSS method can be readily used in other phenomena that follow simple power equations (such as the clustering of galaxies, the discharge of water from drainage systems of different size, the metabolic rate in relation to body biomass, *etc.*). However, a procedure for error estimation has not been developed in this Thesis and therefore the SSS method can not yet be applied to situations where estimation of deviations are required. Instead I have suggested that, on average, predictions made by the SSS approach are within the error limits obtained by model I regression (see Table 3.6).

A second simplifying method for estimating aboveground stand biomass was also presented in Chapter 2. The 'reductionist' model, which was developed in Chapter 2, was used in conjunction with the biomechanical model to readily parameterise Eq.3.1. The reductionist model relates the slope of *M-D* allometry (b) to the slope of *H-D* relationship (b^*) and interpretation of the parametric values in the b-b^* equation was made possible with the analysis provided by fractal geometry (see Section 2.3.2). At this point it should be emphasised that prior to the advent of fractal geometry, spatial dimensions were rarely, if ever, used as a meaningful variable in

ecological research (Zeide, 1993). Within the domain of Euclidean geometry, a standing tree and a sponge possess the same dimension, namely three. However, in fractal geometry each object is characterised by its dimension – which may not be an integer number – that informs us about the inner fabric of the object. The importance of fractal geometry in ecological studies was highlighted by Zeide (1991) who concluded that

'Unlike the geometry of ideal objects, which is the realm of pure mathematics, shapes of natural objects should be studied jointly with the mathematicians and ecologist to the mutual benefit of both disciplines'.

The *b-b** relationship was used in conjunction with the biomechanical model and surprisingly accurate estimations of tree aboveground biomass values at the stand scale were obtained (Table 2.12). However, more research is needed to understand thoroughly the significance of fractal geometry in biomass studies. The traditional approach in estimating standing tree biomass of forest ecosystems requires, more often than not, a vast amount of time and monetary resources. Extrapolation of results, obtained by allometric equations, beyond the site of origin (or for different tree species) generally received with scepticism, and so generalised equations (Pastor *et al.*, 1983/1984; Chapter 3) and pooled regressions were proposed as an alternative to site-specific allometries.

However, these approaches are only partial solutions to the problem of estimating forest biomass, since on one hand, the development of generalised regressions is based on the existence of site-specific models, and on the other, pooled regressions require raw field data collected from a large geographical area. Fractal analysis seems to provide a promising approach to solve the extrapolation problem in biomass studies, since its philosophy is based on the premise that different mechanisms apply to different scales. The fractal dimension of an object (or a phenomenon) is the arithmetic manifestation of the complexity of the object (or the phenomenon), which is directly related to its scale. More interestingly, fractal dimension indicates which mathematical rules should be applied for the study of a particular object (or a

phenomenon). In this Thesis a first attempt to emphasise the significance of fractal geometry in biomass studies has been reported, but it is believed that a much more effort is needed to formulate a more coherent approach. It is possible that fractal analyses may prove useful if combined with remotely sensed data of forest properties.

6.2 ON THE EMPIRICAL PART

Plants and trees assimilate carbon from the atmosphere and produce organic material (biomass) for their survival and growth. The quantity of biomass in a forest is the result of the difference between production through photosynthesis and consumption through respiration, mortality, harvest and herbivory (Kimmins, 1997). Forest biomass changes as a result of succession, management activities, natural disturbances and climatic processes. Thus, according to Brown *et al.* (1999),

'*...biomass is a useful measure for assessing changes in forest structure and a useful measure for comparing structural and functional attributes of forest ecosystems across a wide range of environmental conditions*'.

The most widely-used method for estimating forest biomass is through empirical allometric equations which take the simple form of power function $Y = aX^b$, where a and b are the allometric coefficients that vary with the variables under investigation. Y is the total biomass or one of tree components (stem, branch, foliage, root, *etc.*) and X is a tree dimension variable (usually stem diameter at 1.3 m above ground). Many empirical equations across the globe and for different tree species have been developed.

Studies in the USA (Schroeder *et al.*, 1997; Brown *et al.*, 1999) and Australia/New Zealand (Eamus *et al.*, 2000) have already been conducted to determine the amount of standing biomass in their forest resources. The development and planning of a European database for stem volume and biomass equations for major tree species constitutes a significant component of this Thesis. The database will be useful not

only for forest related studies but to a wide range of research activities covering the areas of global climate change, bioenergy, biodiversity, sustainable management *etc.* The development of the database was initiated within the COST E21 Action '*Contribution of forests and forestry to mitigate greenhouse effects*' funded by EU, in collaboration with colleagues from METLA (Helsinki, Finland). In addition, a global compilation of aboveground biomass allometric equations (Table A1) was also created in order to validate the biomechanical model (Eq. 2.4b) and to develop the SSS method (Chapter 3). The databases will be quite useful in productivity studies since they provide a basic level of information about forest resources.

Understanding the controls on primary productivity of the biosphere is one of the fundamental aims of global change research (Geider *et al.*, 2001). The pivotal contribution to the terrestrial carbon cycle is undisputed since forests store an estimated 360 Pg carbon in living biomass (Dixon *et al.*, 1994). Apart from the importance of tree biomass in environmental studies, Hall (1997) concluded that biomass could be a major contribution to future energy supplies, especially in industrialised countries. According to his study, energy derived from biomass can be used at small and large scales in a decentralised manner, with substantial benefits to rural and urban economies while

'*Growing biomass will provide an economically viable use for land...in Europe and North America*'.

Since southern beech trees show some morpho-physiological differences compared with northern ones (Bussotti *et al.*, 1998), it would not be appropriate to implement mathematical models developed for stands growing in northern and central Europe to the Mediterranean beech forests. Thus, an empirical approach was adopted in an investigation of Naousa municipality forest, Northern Greece, to parameterise biomass allometric relationships. The equations obtained were subsequently used in estimating the variation of aboveground net primary productivity in the study forest.

The aboveground net primary productivity at stand level (P^S) and aboveground growth efficiency (*i.e.*, P^S per unit leaf area) were found to decrease at higher elevations (Figure 5.1 and Table 5.3) and P^S was positively correlated to L^*, which is a crucial component in studies of regional and global phenomena such as global warming, biodiversity and water balance (Waring and Running, 1998). Tree leaf area regulates many forest processes, including gas fluxes, canopy light interception, evapo-transipation and photosynthesis. Jarvis and Leverenz (1983), listed stand L^* as the most important variable in productivity studies and developed a theoretical model that relates P^S to L^*. The parameterisation of this model was based on the amount of the intercepted radiation, the efficiency of a canopy to assimilate CO_2, and the extinction coefficient of intercepted light in a canopy. Their model seems to follow the trend of the empirical pooled data derived for European and Japanese beech stands (Figure 5.4B), when constant values are used for the parameters of the model. However, if a range of parametric values is used in the exponential P^S-L^* model (Jarvis and Leverenz, 1983) corresponding to the canopy structure of different stands, then a series of curves is obtained, fitting more accurately the empirical data. Both experimental and comparative studies have shown that L^*, and in turn net primary productivity, are influenced largely by water and nutrient availability across a variety of coniferous and deciduous forests (Grier and Running, 1977; Birk and Vitousek, 1986; Gower *et al.*, 1992; Matson *et al.*, 1994; Fassnacht and Gower, 1997).

The relation between stable carbon isotope ratio and photosynthetic water-use efficiency (defined as the molar ratio of photosynthetic carbon gain to transpirational water loss) has led to wide spread use of isotopic analysis in plant physiological ecology. Stable carbon isotope composition ($\delta^{13}C$) data were used in order to examine whether trees at the upper limit of the forest are growing under stressful conditions. The stable carbon isotope ratio reflects the balance between mesophyll demand for carbon dioxide against the diffusive supply through the stomata. According to Figure 5.12 less negative $\delta^{13}C$ values were recorded at higher elevations, indicating that overall discrimination against the heavy isotope was

reduced on those sites. Körner *et al.* (1988) concluded that atmospheric variations in $\delta^{13}C$ constitute only a minor proportion of the observed differences in plant tissue composition. The elevational differences in carbon isotope composition appear to reflect real differences in discrimination by plants. Thus, the decline of P^S with increasing altitude indicates that water limitation and/or nutrient deficiency at higher elevations may be the causes for the observed trend. However, since L^* was constant across the beech ecosystem, it is possible that other environmental factors (such as wind) may limit the aboveground growth at higher elevations. Further research focusing on this hypothesis is needed to understand thoroughly the interrelations among environmental variables and net primary production. Data and information for the belowground components are also considered to be of vital importance for a more detailed study of the investigated ecosystem.

Net primary productivity studies will help to improve the assessments of forest-scale carbon (C) exchanges, which in turn can be used to develop better policy decisions related to forest management and conservation. In north-central Greece, models which incorporate environmental and growth variables have not yet been developed. So, on the one hand no information can be drawn for the ecological processes taking place on these valuable resources and on the other hand the forest plans are not based on tools essential for sustainable management. As a result, effects of different silvicultural regimes cannot be predicted and the management of forests is mainly based on the experience of foresters. Thus, the interactions among several ecological functions (water balance, carbon dynamics, nutrient cycling, *etc.*) and anthropogenic disturbances in forest ecosystems should be thoroughly studied. The empirical outcomes of this Thesis (Chapter 4 and Chapter 5) constitute the basis both for further the research in the study beech ecosystem and to develop growth and yields models useful in the management of forest.

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APPENDIX

Table A1: Summary of the 279 allometric regressions found in literature. The following information was recorded from each study: the species and region for which the equation was developed, the values of the allometric parameters, the coefficient of determination, R^2, and the range of the diameter, D, of the harvested trees - whenever this last information was available. The total number of compiled equations is 279. Of these, 62 allometric equations were developed in Australia, 28 in countries from the tropical zone, 20 in Europe and 169 in the USA. The majority of the American equations was obtained from a review paper written by Ter-Mikaelian and Korzukhin (1997). Thirty-three broadleaved species belonging to 15 genera were found in 122 different studies, while 21 coniferous tree species from 8 genera were recorded in 67 studies. In 54 studies, the D interval of the sampled trees was not given, while in two studies estimates of the allometric constant were not reported. The present study is not to be considered an exhaustive review of aboveground biomass equations at a worldwide scale, since a lot of information is believed to exist in 'grey' literature of forestry and related institutes not available to us. Nor is it supposed that a comprehensive examination of scientific papers took place. However, the collected information is assumed to represent an unbiased sample of the population of M-D relationships for tree species growing at the global scale.

No	Author	Region	Species	*a*	*b*	D range (cm)
1	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer rubrum*	0.1262	2.3804	3—66
2	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer rubrum*	0.1789	2.334	10—52
3	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer rubrum*	0.2582	1.6728	0—10
4	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer rubrum*	0.197	2.1933	0—35
5	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer rubrum*	0.1394	2.3405	1—31
6	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer rubrum*	0.1317	2.3199	1—30
7	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer rubrum*	0.1651	2.2394	8—26
8	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer rubrum*	0.1618	2.3095	4—35
9	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer rubrum*	0.091	2.508	5—50
10	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer rubrum*	0.0755	2.5623	5—40
11	Martin *et al.* (1998)	USA	*Acer rubrum*	0.087	2.574	6.3-52.4
12	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer saccharum*	0.1791	2.3329	3—66
13	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer saccharum*	0.1599	2.3376	1—41
14	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer saccharum*	0.1641	2.4209	1—50
15	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer saccharum*	0.2064	2.33	2—40
16	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer saccharum*	0.1252	2.48	2—40
17	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer saccharum*	0.1532	2.3924	1—34
18	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer saccharum*	0.1676	2.3646	4—34
19	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer saccharum*	0.1008	2.5735	5—50
20	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer saccharum*	0.1259	2.52	8—24

21	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer spicatum*	0.204	2.2524	1—20
22	Martin *et al.* (1998)	USA	*All species*	0.0566	2.663	3.8-63
23	Johansson (1999)	Sweden	*Alnus glutinosa*	0.3251	2.022	0-40
24	Johansson (1999)	Sweden	*Alnus incana*	0.1086	2.337	0-36
25	Ter-Mikaelian and Korzukhin (1997)	USA	*Alnus rugosa*	0.2612	2.2087	3—9
26	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula alleghaniensis*	0.1588	2.3376	3—66
27	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula alleghaniensis*	0.1541	2.3666	1—27
28	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula alleghaniensis*	0.1684	2.415	1—55
29	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula alleghaniensis*	0.1188	2.451	3—29
30	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula alleghaniensis*	0.0872	2.587	5—21
31	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula alleghaniensis*	0.154	2.3753	5—50
32	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula lenta*	0.0629	2.6606	5—50
33	Martin *et al.* (1998)	USA	*Betula lenta*	0.0564	2.726	7.8-39.6
34	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula papyrifera*	0.0882	2.562	0—30
35	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula papyrifera*	0.0612	2.6634	3—51
36	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula papyrifera*	0.0775	2.48	2—8
37	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula papyrifera*	0.3154	1.7284	0—15
38	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula papyrifera*	0.1545	2.3064	0—33
39	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula papyrifera*	0.1347	2.3634	1—34
40	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula papyrifera*	0.1074	2.4313	3—33
41	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula papyrifera*	0.1182	2.4287	5—32
42	Wang *et al.* (2000)	USA	*Betula papyrifera*	0.1567	1.879	0.1-13
43	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula populifolia*	0.1564	2.3146	3—24
44	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula populifolia*	0.1218	2.3123	1—23
45	Ter-Mikaelian and Korzukhin (1997)	USA	*Carya spp*	0.0792	2.6349	5—50
46	Ter-Mikaelian and Korzukhin (1997)	USA	*Carya spp*	0.0763	2.6209	5—40
47	Martin *et al.* (1998)	USA	*Carya spp.*	0.0472	2.762	8.2-52.3
48	Leonardi *et al.* (1996)	France	*Castanea sativa*	0.118	2.336	3-23.8
49	Leonardi *et al.* (1996)	Italy	*Castanea sativa*	0.137	2.247	1-36.1
50	Leonardi *et al.* (1996)	Spain	*Castanea sativa*	0.066	2.628	2-16.9
51	Martin *et al.* (1998)	USA	*Cornus florida*	0.0458	2.73	3.8-10.2
52	Ter-Mikaelian and Korzukhin (1997)	USA	*Fagus grandifolia*	0.2013	2.2988	3—66
53	Ter-Mikaelian and Korzukhin (1997)	USA	*Fagus grandifolia*	0.1958	2.2538	2—29

54	Ter-Mikaelian and Korzukhin (1997)	USA	*Fagus grandifolia*	0.1957	2.3916	1—60
55	Ter-Mikaelian and Korzukhin (1997)	USA	*Fagus grandifolia*	0.0842	2.5715	5—50
56	Ter-Mikaelian and Korzukhin (1997)	USA	*Fraxinus americana*	0.1535	2.3213	1—28
57	Ter-Mikaelian and Korzukhin (1997)	USA	*Fraxinus americana*	0.1634	2.348	4—32
58	Ter-Mikaelian and Korzukhin (1997)	USA	*Fraxinus americana*	0.1063	2.4798	5—50
59	Ter-Mikaelian and Korzukhin (1997)	USA	*Fraxinus nigra*	0.1634	2.348	4—32
60	Ter-Mikaelian and Korzukhin (1997)	USA	*Liriodendron tulipifera*	0.0365	2.7324	5—50
61	Ter-Mikaelian and Korzukhin (1997)	USA	*Liriodendron tulipifera*	0.0687	2.5153	5—40
62	Martin *et al.* (1998)	USA	*Liriodendron tulipifera*	0.0580	2.635	10.2-55.8
63	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus grandidentata*	0.0983	2.3773	1—34
64	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus grandidentata*	0.0785	2.4981	3—45
65	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus tremuloides*	0.1008	2.4341	1—30
66	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus tremuloides*	0.079	2.3865	1—32
67	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus tremuloides*	0.0911	2.2759	1—26
68	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus tremuloides*	0.0774	2.3466	5—33
69	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus tremuloides*	0.0637	2.6087	3—51
70	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus tremuloides*	0.1625	2.0673	0—15
71	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus tremuloides*	0.1049	2.391	0—36
72	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus tremuloides*	0.0928	2.4085	1—27
73	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus tremuloides*	0.0726	2.4827	2—33
74	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus tremuloides*	0.0527	2.5084	3—50
75	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus tremuloides*	0.1231	2.242	3—36
76	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus tremuloides*	0.2065	2.249	15—40
77	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus tremuloides*	0.1122	2.35	1—32
78	Ter-Mikaelian and Korzukhin (1997)	USA	*Prunus pensylvanica*	0.1556	2.1948	3—24
79	Ter-Mikaelian and Korzukhin (1997)	USA	*Prunus pensylvanica*	0.2159	1.7041	0—10
80	Ter-Mikaelian and Korzukhin (1997)	USA	*Prunus serotina*	0.0716	2.6174	5—50
81	Ter-Mikaelian and Korzukhin (1997)	USA	*Prunus serotina*	0.1225	2.4253	5—40
82	Ter-Mikaelian and Korzukhin (1997)	USA	*Prunus virginiana*	0.2643	1.7102	3—15
83	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus alba*	0.2022	2.1666	0—18
84	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus alba*	0.0293	2.8661	8—26
85	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus alba*	0.0579	2.6887	5—50
86	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus alba*	0.0472	2.701	5—40

87	Martin *et al.* (1998)	USA	*Quercus alba*	0.0542	2.613	7-63.01
88	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus coccinea*	0.2482	2.19	0—23
89	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus coccinea*	0.0536	2.7147	8—28
90	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus coccinea*	0.1241	2.4395	5—40
91	Martin *et al.* (1998)	USA	*Quercus coccinea*	0.0521	2.685	15-43.3
93	Canadell *et al.* (1988)	Spain	*Quercus ilex*	0.4864	1.9	5.3-19.8
94	Canadell *et al.* (1988)	Spain	*Quercus ilex*	0.1399	2.413	5.3-24.4
95	Canadell *et al.* (1988)	Spain	*Quercus ilex*	0.2208	2.217	5.3-24.4
96	Canadell *et al.* (1988)	Spain	*Quercus ilex*	0.5308	1.831	5.3-30
97	Canadell *et al.* (1988)	Spain	*Quercus ilex*	0.1253	2.433	6.6-24.4
92	Susmel *et al.* (1976)	Italy	*Quercus ilex*	0.2302	2.28	20-90
98	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus macrocarpa*	0.1447	2.282	6—25
99	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus prinus*	0.0554	2.7276	5—50
100	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus prinus*	0.0907	2.5344	5—40
101	Martin *et al.* (1998)	USA	*Quercus prinus*	0.0258	2.91	10.6-57.5
102	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus rubra*	0.1335	2.422	5—34
103	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus rubra*	0.113	2.4572	5—50
104	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus rubra*	0.0643	2.6598	5—40
105	Martin et al. (1998)	USA	*Quercus rubra L.*	0.0550	2.644	19.7-52
106	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus velutina*	0.0904	2.5143	7—27
107	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus velutina*	0.0945	2.503	5—40
108	Ter-Mikaelian and Korzukhin (1997)	USA	*Salicaceae*	0.1619	2.0552	3—24
109	Ter-Mikaelian and Korzukhin (1997)	USA	*Salicaceae*	0.0616	2.5094	4—20
110	Ter-Mikaelian and Korzukhin (1997)	USA	*Ulmus americana*	0.0825	2.468	4—29
111	Ter-Mikaelian and Korzukhin (1997)	USA	*Abies amabilis*	0.0627	2.4921	31—90
112	Ter-Mikaelian and Korzukhin (1997)	USA	*Abies balsamea*	0.0877	2.4017	3—51
113	Ter-Mikaelian and Korzukhin (1997)	USA	*Abies balsamea*	0.0523	2.53	3—25
114	Ter-Mikaelian and Korzukhin (1997)	USA	*Abies balsamea*	0.3908	1.6217	0—20
115	Ter-Mikaelian and Korzukhin (1997)	USA	*Abies balsamea*	0.1746	2.1555	0—36
116	Ter-Mikaelian and Korzukhin (1997)	USA	*Abies balsamea*	0.1075	2.3263	3—28
117	Ter-Mikaelian and Korzukhin (1997)	USA	*Abies balsamea*	0.1598	2.1283	2—32
118	Ter-Mikaelian and Korzukhin (1997)	USA	*Abies balsamea*	0.2575	2.0543	3—40
119	Ter-Mikaelian and Korzukhin (1997)	USA	*Abies balsamea*	0.069	2.4975	3—40

120	Ter-Mikaelian and Korzukhin (1997)	USA	*Abies balsamea*	0.0705	2.497	4—34
121	Wang *et al.* (2000)	USA	*Abies lasiocarpa*	0.0817	2.24	1-8.2
122	Ter-Mikaelian and Korzukhin (1997)	USA	*Chamaecyparis nootkatensis*	0.2498	2.1118	18—60
123	Ter-Mikaelian and Korzukhin (1997)	USA	*Larix laricina*	0.1265	2.2453	3—51
124	Ter-Mikaelian and Korzukhin (1997)	USA	*Larix laricina*	0.1359	2.298	7—30
125	Ter-Mikaelian and Korzukhin (1997)	USA	*Larix laricina*	0.0946	2.3572	2—31
126	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea abies*	0.2722	2.104	12—44
127	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea glauca*	0.0777	2.472	1—33
128	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea glauca*	0.0635	2.48	3—25
129	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea glauca*	0.1077	2.3308	0—39
130	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea glauca*	0.1601	2.2413	2—30
131	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea glauca*	0.1037	2.2907	2—32
132	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea glauca*	0.1643	2.248	2—25
133	Barney *et al.* (1978)	USA	*Picea mariana*	0.0331	2.59	1.4-8.5
134	Barney *et al.* (1978)	USA	*Picea mariana*	0.0377	2.54	1.4-12.9
135	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea mariana*	0.153	2.248	1—23
136	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea mariana*	0.1444	2.2604	0—37
137	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea mariana*	0.2626	2.0707	2—30
138	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea mariana*	0.1683	2.1777	2—34
139	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea mariana*	0.0963	2.4289	3—32
140	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea mariana*	1.3836	1.544	2—15
141	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea mariana*	0.0339	2.626	2—15
142	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea mariana*	0.1137	2.316	2—25
143	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea rubens*	0.6149	1.5639	0—20
144	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea rubens*	0.1444	2.2604	0—37
145	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea rubens*	0.2066	2.183	1—35
146	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea rubens*	0.166	2.2417	1—31
147	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus banksiana*	0.2131	2.1283	0—38
148	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus banksiana*	0.2186	1.94	0—20
149	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus banksiana*	0.1093	2.3291	3—34
150	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus banksiana*	0.0919	2.4206	2—32
151	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus banksiana*	0.1747	2.2495	6—39
152	Zavitkovsi *et al.* (1981)	USA	*Pinus banksiana*	0.1055	2.2738	4-19

153	Zavitkovsi *et al.* (1981)	USA	*Pinus banksiana*	0.1410	2.2278	4-18
154	Son *et al.* (2001)	Korea	*Pinus koraiensis*	0.1393	2.386	7-35.5
155	Forrest (1969)	Australia	*Pinus radiata*	0.2671	1.727	1.4-5.8
156	Forrest (1969)	Australia	*Pinus radiata*	0.0535	2.318	10.3-19.8
157	Forrest (1969)	Australia	*Pinus radiata*	0.0481	2.663	6.4-14.5
158	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus resinosa*	0.1003	2.3865	3—51
159	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus resinosa*	0.0847	2.3503	2—34
160	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus resinosa*	0.0778	2.4171	3—46
161	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus rigida*	0.104	2.3373	0—31
162	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus strobus*	0.0696	2.449	3—66
163	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus strobus*	0.1617	2.142	2—37
164	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus strobus*	0.6298	1.3475	0—15
165	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus strobus*	0.0755	2.3833	5—26
166	Ovington (1957)	UK	*Pinus sylvestris*	0.0398	2.64	0.5-22.7
167	Santa Regina *et al.* (1997)	Spain	*Pinus sylvestris*	0.2206	2.0519	2.5-36.5
168	vanLear *et al.* (1984)	USA	*Pinus taeda*	0.0695	2.5641	12.7-38.6
169	Bartelink (1996)	Netherland	*Pseudotsuga menziesii*	0.1978	2.41	6.9-28.5
170	Ter-Mikaelian and Korzukhin (1997)	USA	*Pseudotsuga menziesii*	0.0808	2.5282	5—54
171	Ter-Mikaelian and Korzukhin (1997)	USA	*Thuja occidentalis*	0.2305	1.9269	3—51
172	Ter-Mikaelian and Korzukhin (1997)	USA	*Thuja occidentalis*	0.1148	2.1439	2—30
173	Ter-Mikaelian and Korzukhin (1997)	USA	*Thuja occidentalis*	0.091	2.234	4—31
174	Ter-Mikaelian and Korzukhin (1997)	USA	*Tilia americana*	0.0872	2.3539	4—47
175	Ter-Mikaelian and Korzukhin (1997)	USA	*Tilia americana*	0.0617	2.5328	5—50
176	Ter-Mikaelian and Korzukhin (1997)	USA	*Tsuga canadensis*	0.0991	2.3617	3—51
177	Ter-Mikaelian and Korzukhin (1997)	USA	*Tsuga canadensis*	0.1617	2.1536	2—34
178	Ter-Mikaelian and Korzukhin (1997)	USA	*Tsuga canadensis*	0.0622	2.45	5—50
179	Ter-Mikaelian and Korzukhin (1997)	USA	*Tsuga heterophylla*	0.257	2.1349	16—49
180	Ter-Mikaelian and Korzukhin (1997)	USA	*Tsuga mertensiana*	0.5038	2.0154	44—76
181	Clough and Scott (1989)	Australia	*Bruguiera gymnorrhiza*	0.1858	2.3055	2.0-24
182	Clough and Scott (1989)	Australia	*Bruguiera parviflora*	0.1679	2.4167	2.0-21
183	Clough and Scott (1989)	Australia	*Ceriops targal var. australis*	0.1884	2.3379	2.0-18
184	Eamus *et al.* (2000)	Australia	*Erythrophloem chlorostachys*	0.0407	2.851	4.6-14.7
185	Eamus *et al.* (2000)	Australia	*Eucalyptus*	0.162	2.383	2.6-52.8

186	Eamus *et al.* (2000)	Australia	*Eucalyptus bleeseri*	0.1366	2.497	4.6-22.7
187	Ward and Pikersgill (1985)	Australia	*Eucalyptus calophylla*	0.3985	1.64	2-11.5
188	Ward and Pikersgill (1985)	Australia	*Eucalyptus calophylla*	0.2143	2.04	2-24.5
189	Eamus *et al.* (2000)	Australia	*Eucalyptus combined*	0.4506	2.082	3.15-60.34
190	Eamus *et al.* (2000)	Australia	*Eucalyptus combined*	0.1092	2.468	6.68-24.77
191	Grove and Malajczuk (1985)	Australia	*Eucalyptus diversicolor*	0.1179	2.47	2-40
192	Bennett *et al.* (1997)	Australia	*Eucalyptus globulus*	0.1466	2.3	7.5-22.8
193	Applegate (1982)	Australia	*Eucalyptus intermedia*	0.0394	2.6018	13.4-25.5
194	Ward and Pikersgill (1985)	Australia	*Eucalyptus maculata*	0.3328	1.87	2-11.5
195	Ward and Pikersgill (1985)	Australia	*Eucalyptus maculata*	0.0812	2.47	2-24.5
196	Eamus *et al.* (2000)	Australia	*Eucalyptus miniata*	0.1581	2.426	2.6-50
197	Eamus *et al.* (2000)	Australia	*Eucalyptus miniata*	0.2352	2.269	2.6-50
198	Eamus *et al.* (2000)	Australia	*Eucalyptus miniata*	0.7103	1.925	2.6-50
199	Keith *et al.* (cited in Keith *et al.* 2000)	Australia	*Eucalyptus obliqua*	0.1287	2.353	25.4-78
200	Keith *et al.* (cited in Keith *et al.* 2000)	Australia	*Eucalyptus obliqua*	0.0644	2.584	29.9-70.8
202	Keith *et al.* (cited in Keith *et al.* 2000)	Australia	*Eucalyptus obliqua*	0.0350	2.642	21.1-55.3
203	Keith *et al.* (cited in Keith *et al.* 2000)	Australia	*Eucalyptus obliqua*	0.2023	2.283	26.2-284
204	Snowdon *et al.* (2000)	Australia	*Eucalyptus obliqua*	0.0929	2.445	19.95-186
205	Eamus *et al.* (2000)	Australia	*Eucalyptus papuana*	0.0437	2.79	11.7-44.2
201	Applegate (1982)	Australia	*Eucalyptus pilularis*	0.0464	2.6934	13.1-123.9
206	Applegate (1982)	Australia	*Eucalyptus pilularis*	0.0491	2.6803	17.8-53.4
207	Eamus *et al.* (2000)	Australia	*Eucalyptus porrecta*	0.0811	2.512	7.5-24.9
208	Ward and Pikersgill (1985)	Australia	*Eucalyptus resinifera*	0.3262	1.74	2-11.5
209	Ward and Pikersgill (1985)	Australia	*Eucalyptus resinifera*	0.0788	2.44	2-24.5
210	Eamus *et al.* (2000)	Australia	*Eucalyptus tetrodonta*	0.1774	2.351	2.7-52.10
211	Eamus *et al.* (2000)	Australia	*Eucalyptus tetrodonta*	0.1861	2.348	2.7-52.8
212	Eamus *et al.* (2000)	Australia	*Eucalyptus tetrodonta*	0.4686	2.083	2.7-52.9
213	Martin *et al.* (1998)	USA	*Oxydendrum arboreum*	0.0605	2.582	4.3-34.6
214	Eamus *et al.* (2000)	Australia	*Terminalia ferdinandiana*	0.1914	2.263	2.6-16.7
215	Eamus *et al.* (2000)	Australia	*tropical*	0.0720	2.644	4-29.1
216	Eamus *et al.* (2000)	Australia	*tropical*	0.1349	2.622	2.7-22.1
217	Nelson *et al.* (1999)	Brazil	*tropical*	0.1357	2.4128	1.2-28.6
218	Nelson *et al.* (1999)	Brazil	*tropical*	0.1627	2.37	1.2-26.8

219	Nelson *et al.* (1999)	Brazil	*tropical*	0.0811	2.4257	5.1-38.2
220	Nelson *et al.* (1999)	Brazil	*tropical*	0.0671	2.5996	2.3-25.3
221	Nelson *et al.* (1999)	Brazil	*tropical*	0.1657	2.4206	1.5-12.2
222	Nelson *et al.* (1999)	Brazil	*tropical*	0.1081	2.5105	1.6-24.8
223	Nelson *et al.* (1999)	Brazil	*tropical*	0.0934	2.5392	1.6-21.8
224	Nelson *et al.* (1999)	Brazil	*tropical*	0.1681	2.3651	1.5-28.6
225	Clough and Scott (1989)	Australia	*Xylocarpus granatum*	0.0823	2.5883	3.0-17
226	Kumar *et al.* (1998)	India	*Acacia auriculiformis*	0.2061	2.4369	n/a
227	Kumar *et al.* (1998)	India	*Acacia auriculiformis*	0.2746	2.3052	n/a
228	Morrison (1990)	USA	*Acer saccharum*	0.5018	2.0444	n/a
229	Hughes (1971)	UK	*Alnus glutinosa*	0.0859	2.35371	n/a
230	Kumar *et al.* (1998)	India	*Artocarpus heterophyllus*	0.1792	2.2512	n/a
231	Kumar *et al.* (1998)	India	*Artocarpus hirsutus*	0.0464	2.7934	n/a
232	Snowdon *et al.* (2000)	Australia	*Australian plantation*	0.1059	2.3582	n/a
233	Westman and Rogers (1977)	Australia	*Banksia aemula*	0.0528	2.5924	n/a
234	Hingston *et al.* (1981)	Australia	*Banksia grandis*	0.1043	2.5	n/a
235	Glossop (1978)	Australia	*Banksia grandis*	0.1152	2.4383	n/a
236	Morrison (1990)	USA	*Betula alleghaniensis*	0.3168	2.1307	n/a
237	Hughes (1971)	UK	*Betula pendula*	0.2511	2.2865	n/a
238	Kumar *et al.* (1998)	India	*Casuarina equistifolia*	0.1040	2.7142	n/a
239	Hingston *et al.* (1981)	Australia	*Eucalyptus calophylla*	0.0343	2.74	n/a
240	Glossop (1978)	Australia	*Eucalyptus calophylla*	0.1458	1.1536	n/a
241	Grove and Malajczuk (1985)	Australia	*Eucalyptus diversicolour*	0.0535	2.74	n/a
242	O' Brien (1998)	Australia	*Eucalyptus grandis*	0.4458	1.771	n/a
243	O' Brien (1998)	Australia	*Eucalyptus grandis*	0.1077	2.404	n/a
244	Barrett (1992)	Australia	*Eucalyptus maculata*	0.1905	2,43	n/a
245	Hingston *et al.* (1981)	Australia	*Eucalyptus marginata*	0.0252	2.84	n/a
246	Todd (2000)	Australia	*Eucalyptus marginata*	0.0241	3.0499	n/a
247	Todd (2000)	Australia	*Eucalyptus marginata*	0.0271	3.2306	n/a
248	Todd (2000)	Australia	*Eucalyptus marginata*	0.0872	2.4882	n/a
249	Glossop (1978)	Australia	*Eucalyptus marginata*	0.0353	1.4219	n/a
250	Ward and Koch (1996)	Australia	*Eucalyptus resinifera*	0.0934	2.4	n/a
251	Bartelink (1997)	Netherlands	*Fagus sylvatica*	0.0798	2.601	n/a

252	Santa Regina *et al.* (1997)	Spain	*Fagus sylvatica*	0.1326	2.4323	n/a
253	Grove (1988)	Australia	*Karri*	0.1717	2.128	n/a
254	Kumar *et al.* (1998)	India	*Paraserianthes falcataria*	0.0538	2.6818	n/a
255	Snowdon *et al.* (2000)	Australia	*Pine plantation*	0.1179	2.2476	n/a
256	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus banksiana*	0.152	2.273	n/a
257	Green and Grigal (1978)	USA	*Pinus banksiana*	n/a	2.38	n/a
258	Zavitkovsi and Dawson (1978)	USA	*Pinus banksiana*	n/a	2.19	n/a
259	Lieffers and Campbell (1984)	USA	*Populus tremuloides*	0.1007	2.4343	n/a
260	Kumar *et al.* (1998)	India	*Pterocarpus marsupium*	0.0410	2.8286	n/a
261	Leonardi and Rapp (1982)	Italy	*Quercus ilex*	0.2187	2.0491	n/a
262	Ferres *et al.* (1980)	Spain	*Quercus ilex*	0.2319	2.265	n/a
263	Snowdon *et al.* (2000)	Australia	Rainforest	0.1500	2.3698	n/a
264	Barrett (1992)	Australia	Rainforest species	0.2344	2.34	n/a
265	Clough and Scott (1989)	Australia	Rhyzophora apiculata/stylosa	0.1049	2.6848	n/a
266	Snowdon *et al.* (2000)	Australia	Sclerophyll forest	0.1446	2.3501	n/a
267	Brown (1997)	Brazil	Tropical	0.0880	2.57	n/a
268	Higuchi *et al.* (1998)	Brazil	Tropical	0.1353	2.55	n/a
269	Araujo *et al.* (1999)	Brazil	Tropical	0.0780	2.65	n/a
270	Brown (1997)	Brazil	Tropical	0.1043	2.66	n/a
271	Brown (1997)	Cambodia	Tropical	0.0916	2.56	n/a
272	Overman *et al.* (1994)	Colombia	Tropical	0.1394	2.48	n/a
273	Brown (1997)	Costa Rica	Tropical	0.1636	2.32	n/a
274	Lescure *et al.* (1983)	Fr. Guiana	Tropical	0.0561	2.72	n/a
275	Brown (1997)	Indonesia	Tropical	0.1043	2.6	n/a
276	Ketterings *et al* (2001)	Indonesia	Tropical	0.0661	2.591	n/a
277	Edwards and Grubb (1977)	New Guinea	Tropical	0.1353	2.36	n/a
278	Ovington (1957)	Puerto Rico	Tropical	0.0898	2.41	n/a
279	Snowdon *et al.* (2000)	Australia	Woodland trees	0.2350	2.2364	n/a

Table A.2: The two-way analysis of variance for the $\ln\sigma$ values calculated for the nine sample trees. Analysis on the untransformed data indicated that the error variance of σ was not equal across groups. The analysis is based on data calculated for three crown classes (top, middle and bottom). The model is $\ln\sigma = I + C_D + E_C$ where I denotes the intercept, C_D the crown depth and E_C the elevation class, respectively. The coefficient of determination is 0.68.

	Sum of squares	*df*	*Mean square*	*F*	*P*
Corrected	2.28	8	0.285	12.18	< 0.001
Intercept	1442.85	1	1442.85	61672.06	< 0.001
ELEVATION CLASS	1.8	2	0.90.1	38.49	< 0.001
CROWN DEPTH	0.42	2	0.21	8.96	< 0.001
Interaction	0.0595	4	0.0148	0.63	> 0.60
Residual	1.053	45	2.34×10^{-2}		
Total error	1446.18	54			

Table A.3: The analysis of variance table for the influence of interaction between crown depth and elevation on the values of $\delta^{13}C$ for the nine sample trees. The model is $\delta^{13}C = I + C_D + E_C + C_D \times E_C$ where I denotes the intercept, C_D the crown depth and E_C the elevation class, respectively. The coefficient of determination is 0.70.

	Sum of squares	*df*	*Mean square*	*F*	*P*
Corrected	67.88	8	8.48	13.27	< 0.001
Intercept	43122.49	1	43122.49	67461.9	< 0.001
ELEVATION CLASS	65.87	2	32.93	51.52	< 0.001
CROWN DEPTH	1.77	2	0.889	1.39	> 0.25
Interaction	0.232	4	0.058	0.091	> 0.98
Residual	28.76	45	0.63		
Total error	43219.14	54			

Table A4: The two-way analysis of variance table for the influence of crown depth and elevation on the values of **A)** N_A. The model is $N_A = I + C_D + E_C + C_D \times E_C$ and $R^2 = 0.50$. **B)** N_M. . The model is $N_A = I + C_D + E_C + C_D \times E_C$ and $R^2 = 0.06$. I denotes the intercept, C_D the crown depth and E_C the elevation class, respectively.

A: *Nitrogen per unit area*	***Sum of squares***	***df***	***Mean square***	*F*	*P*
Elevation class	5.1×10^{-8}	2	2.55×10^{-8}	24.2	< 0.001
Crown depth	9.85×10^{-9}	2	4.92×10^{-9}	4.67	> 0.01
Interaction	4.8×10^{-9}	4	1.21×10^{-9}	1.15	> 0.30
Residual	4.74×10^{-8}	45	1.05×10^{-9}		
Total error	10^{-6}	54			

B: *Nitrogen per unit mass*	***Sum of squares***	***df***	***Mean square***	*F*	*P*
Elevation class	9.21×10^{-5}	2	4.6×10^{-5}	3.92	< 0.05
Crown depth	4.08×10^{-6}	2	2.04×10^{-6}	0.17	> 0.80
Interaction	4.31×10^{-5}	4	1.07×10^{-5}	0.91	> 0.45
Residual	5.28×10^{-4}	45	1.17×10^{-5}		
Total error	2.57×10^{-2}	54			